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By

Nicholas George Spano

A dissertation submitted in partial satisfaction of the

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in

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in the

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of the

University of California, Berkeley

Committee in charge:

Professor Anthony D. Barnosky, Chair Professor Cynthia V. Looy Professor Thomas Bruns

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Abstract

Assessing indicators of population size and causes of extinction in late Quaternary megafauna

By

Nicholas George Spano

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Professor Anthony D. Barnosky, Chair

Megafauna are ecologically important. They are ecosystem engineers that substantially modify modern ecosystems, and likely did so for prehistoric ecosystems prior to the Late Quaternary extinction (LQE) event as well. The LQE resulted in the loss of ~65% of all large mammals during an age of global climate change and human population expansion. This means that understanding the causes and ecological impacts of megafauna preceding, during, and following the LQE is important for better understanding megafauna ecology and conservation today.

To further this understanding, here I 1) explore the developing body of indicators used for inferring historic and prehistoric megafauna abundances; 2) investigate the environmental conditions surrounding human arrival and megafauna extirpation in Brazil, and; 3) test how sensitive the *Sporormiella* megafauna indicator is to temperature and humidity, as these factors could confound megafaunal population-size estimates based on *Sporormiella* abundances.

The first chapter reviews the many different population-size indicators used in megafauna paleoecology. and finds all have their pros and cons regarding their applicabilities towards reconstructing megafauna populations depending on the depositional environment and other taphonomic factors. A widely used indicator of relative megafauna population size is the abundance of the dung fungus *Sporormiella* in sediment records, despite the need for more taphonomic work necessary to more robustly relate spore abundance to megafauna abundance.

The second chapter untangles the relationship between climate, vegetation changes, human population growth, and megafauna decline surrounding the LQE in Brazil as a case study. I found that combinations of anthropogenic, climatic, and vegetational changes are likely implicated as causal factors, but the tree factors vary in their importance for different regions of Brazil. However, human population growth prior to the megafauna extirpation stands out as most notable.

The third chapter reports results of an experiment that tested the effects of temperature and relative humidity on *Sporormiella* growth. I found that humidity above 89% does not notably affect *Sporormiella* growth but temperature in the range of 10-40°C is important.

In sum, this means that there is room for development of megafauna indicators, nuances between how different LQE causes can be distinguished at finer spatial scales, and reason to suggest that past climate change may bias *Sporormiella*-based reconstructions of megafauna populations.

Chapter 1: A review of terrestrial vertebrate paleo-presence and -abundance indicators

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Abstract

Terrestrial vertebrate paleo-presence and -abundance indicators are indirect measures of past vertebrate occupation at or around a depositional site. They include a broad set of indicators that have been used for various archaeological, paleoecological, and historic applications, but an integrated review of their pros, cons, and efficacy has been lacking. Here I provide such a review that includes fungal spores, steroidal biomarkers, paleoenvironmental DNA, pollen and plant spore types associated with vertebrates, radiometric date clusters from bone records, invertebrate remains, and other miscellaneous past vertebrate population density indicators. Although much remains unknown about the taphonomy and fidelity of these vertebrate population indicators, this review highlights a great potential for actualistic experiments, advances in identification tools, and additional applications to further our understanding of these novel sources of information about past vertebrate populations.

Introduction

Terrestrial vertebrate paleo-population-density indicators (PDIs) are indirect markers of past vertebrate population densities, in contrast to more direct observational methods that can be applied to living biota. This is a precise definition that encompasses a group of indicators that have been reviewed separately (e.g., Rawlence et al., 2014; Perrotti & van Asperen, 2019) but not yet in an integrated way. Evaluating these indicators together provides a better understanding about their potential applications, including: reconstructing Quaternary faunal communities (Lydolph et al.,

2005); reconstructing historic pastoral landscapes (Chepstow-Lusty et al., 2019; Etienne et al., 2015; Giguet-Covex et al., 2014; Guillemot et al., 2015); pinpointing Hannibal's path through the Alps en route to invading Italy (Mahaney et al., 2017); and the timing of extinctions during the Quaternary. These latter applications include both Holocene insular extinctions (Wood et al., 2011; Graham et al., 2016; Burney, Robinson, & Burney, 2003) and late Pleistocene examples (Halligan et al., 2016). Along with determining the timing of Quaternary extinctions, some studies have applied these PDIs to document ecological state-shifts following Quaternary defaunation (Gill et al., 2009; Rule et al., 2012; Barnosky et al., 2016; Robinson, G. S., Pigott Burney, L., & Burney, 2005).

PDIs and paleoenvironmental indicators are commonly preserved alongside each other and can thus provide complementary sources of information for more complete paleoenvironmental reconstructions. For example, by combining records of dung fungal spores with pollen records, we can better understand the establishment of animal husbandry practices through time (Setyaningsih et al., 2019) and the evolution of pastoral landscapes (Guillemot et al., 2015; López-Merino et al., 2009; Schofield & Edwards, 2009). These synoptic studies can also help to inform debates regarding the causes of late-Quaternary extinctions by more precisely timing vertebrate last appearances in comparison with environmental changes (e.g., Fiedel, 2018). In associated research areas, PDIs can help inform long-term perspectives on landscape restoration and ecological baseline assessment through enabling inferences about vertebrate paleo-population-densities with their associated habitats (Bradshaw, Hannon, & Lister, 2003; Vera, 2000; Birks, 2005). PDIs can also potentially provide insights regarding pre-Quaternary terrestrial vertebrate-ecosystem dynamics, as many of these PDIs were present before the Quaternary (e.g., Davis & Ellis, 2010; Andreev et al., 2014)

Survey methodology

My literature search included three queries through Web of Science with all available databases and articles published from 1864 - 2019 and the following search terms on 16 October 2019:

For indicator fungal spores:

TS=(((pal\$eo* OR arch\$eolog* OR histor*) AND (((dung OR coprophilous OR keratin*) AND fung* AND spore\$) OR sporormiella)))

For indicator plant spores/pollen:

TS=(((pal\$eo* OR arch\$eolog* OR histor*) AND (palyno* OR pollen\$) AND (livestock OR pastor* OR megafauna\$ OR grazer\$) AND (indicator\$ OR proxy OR proxies)))

This query returned 144 articles on the *Sporormiella* (synonym: *Preussia*) indicator. The bibliographies of relevant publications were then mined to further identify pertinent articles. Here I generally cite only the most comprehensive or recent articles, but many additional relevant references can be found in review articles cited within this review (e.g., Perrotti & van Asperen, 2019; Evershed & Bethell, 1996; Rawlence et al., 2014; and references therein).

Defining terrestrial vertebrate paleo-population-density indicators

Although this review focuses on terrestrial vertebrate paleo-population-density indicators, some of those covered here (e.g., steroidal biomarkers, pollen types associated with vertebrates, radiometric date clusters from bone records, and helminth (parasitic worm) eggs) have so far only been applied to infer vertebrate presence. Complications in using these indicators to infer vertebrate population density include taphonomic pathways that may be largely unknown and that can bias the population estimate unduly. Thus, I provide this caveat that many of the indicators discussed here are still largely undeveloped, but may well reflect terrestrial population densities and have the potential to be further refined.

I limit this review to terrestrial vertebrates because the field of aquatic vertebrate paleo-population-density indicators is relatively unestablished, aside from historical quantitative studies that use fisheries records to infer fish population densities (see Jackson & McClenachan, 2017). Similarly, relatively little information is available about non-vertebrate paleo-population-density indicators relative to the situation for vertebrates. However, paleoenvironmental DNA (PalEnDNA) studies could provide insights for reconstructing populations of invertebrate and plant communities (Rawlence et al., 2014).

In the context of this paper, the "paleo" in PDIs is more of a methodological definition than a temporal one, given that the temporal extent of included studies ranges from centuries (e.g., Etienne et al., 2015) to potentially more than 65 million years (e.g., Schweiger & Svenning, 2018). Regarding population density, all paleo-indicators are spatially- and temporally-averaged to some

degree, so to reflect this, I use the term population density to indicate the average number of individuals per unit area instead of overall population size. I refer to these remains as indicators instead of proxies because proxies are assumed to be direct substitutes for their given forcing variable(s) (Cohen, 2003, p. 4). Many of these indicators have not yet been tested enough to be *bona fide* direct substitutes for terrestrial vertebrate paleo-population densities. My intent in this review is to provide an overview of the PDIs, taphonomic considerations that may affect them, and future directions to potentially strengthen these indicators towards better reconstructing terrestrial vertebrate paleo-population densities.

Indicators

This review focuses on a broad set of organic remains that can be preserved in sediments, including fungal spores, steroidal biomarkers, paleoenvironmental DNA (PalEnDNA), pollen types associated with vertebrates, radiometric date clusters from bone records, invertebrate remains (including those from dung beetles, dung-inhabiting mites, and helminth eggs), and other miscellaneous PDIs (Fig. 1). Summarized information regarding their population density fidelities, taxa each indicator has been associated with, host-taxon precisions, depositional environments, relative preservation potentials, and applications is available in the literature (see Table 1 for an overview).

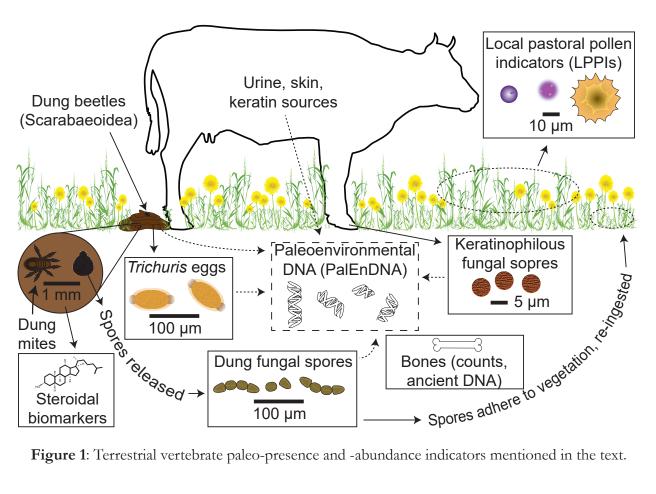


Figure 1: Terrestrial vertebrate paleo-presence and -abundance indicators mentioned in the text.

Table 1: Characteristics of terrestrial vertebrate paleo-population density indicators

Coprophilous fungi (Sporormiella (syn: Preussia), Sordaria, Podospora)	General indicator
Assumed to be high but requires more understandin g	Population density fidelity
Mammals and birds	Taxa the indicator has been associated with
Medium- high	Host-taxon precision
Lacustrine sediments, peatland sediments, marine sediments, soils, and dung	Depositional environments
High	Relative preservation potential
Linking late-Quaternary extinctions with environmental change; reconstructing pastoral landscapes	Paleo applications
Aptroot & van Geel, 2006; Baker, Bhagwat, & Willis, 2013; Chepstow-Lusty et al., 2019; Davis, 1987; Ekblom & Gillson, 2010; Graham et al., 2016; Guillemot et al., 2015; Ledger et al., 2014; Perrotti & van Asperen, 2019; and references therein	References

Steroidal biomarkers	Keratinophilous fungi
Unknown	Unknown
Mammals	Mammals, arthropods, and birds
Medium	Unknown or low
Dung, soils, mire sediments, and aquatic sediments	Caves, cold sediments, marine sediments, and archaeological soils
Medium to high	Unknown or low to mediumlow
Identifying fecal material in archaeological soils; lipid analysis of a ground sloth coprolite; timing Hannibal's invasion of Italy; documenting historic fecal pollution in lake sediments; testing a putative 14,000 year-old human coprolite from Oregon; reconstructing a	Proposed megafaunal indicator associated with mammoth, bison, and horse DNA in permafrost; proposed indicator of anthropogenically- altered Medieval settlements in Russia and Kazakhstan
Evershed, 1993; Evershed & Bethell, 1996; Gill et al., 2009; Guillemot et al., 2015; Mahaney et al., 2017; Müller et al., 1979; Sistiaga et al., 2014; and references therein	Cano & Guarro, 1990; Ginarte et al., 1996; Hayes, 2012; Howard, 2002; Ivanova & Marfenina, 2015; Presbury & Young, 1978; Van Oorschot & Connie, 1980; Zhang et al., 2006; Zimmermann, 2008

pastoral landscape from Greenland

Pastoral pollen indicators (PPIs)	Paleoenvironmental DNA (PalEnDNA)
Unknown	Unknown
Mammalian livestock	Many
Unknown	Medium
Soils	Many
High	Medium
Reconstructing pastoral landscapes	Reconstructing paleoenvironmental histories; timing megafaunal extirpations; taxonomic surveys; reconstructing pastoral landscapes
Florenzano et al., 2015; Gauthier et al., 2010; Ledger et al., 2014; Ledger, Edwards, & Schofield, 2015; Mercuri & Carter, 2013; Qiu et al., 2014; van Geel et al.,	Etienne et al., 2015; Graham et al., 2016; Hadly et al., 2004; Parducci et al., 2017; Rawlence et al., 2014; Ramakrishnan et al., 2005; and references therein

Mites (Orders: Oribatida and Gamasina)	Dung beetles	Fossil bones
Unknown	Unknown	Medium to good, depending on sample size, taxa, and taphonomy
Humans, livestock, and poultry	Extinct megafauna (inferred) and domesticate d mammals	Many
Medium (Gamasina) or unknown	Unknown	Large vertebrates: Poor to medium Small vertebrates: Medium to high (depending on depositional system)
Pasture soils, lake sediments, and archaeological dung deposits	Dung, soils	Coastal, fluvial/deltaic, lacustrine, volcanigenic, eolian, et al
Medium	Low	High
Identifying archaeological dung deposits; timing the rise and fall of the Inca empire with	Landscape shifts following Quaternary large herbivore extinctions in the UK; environmental reconstruction of a Roman archaeological site in the Netherlands	Linking late-Quaternary extinctions with environmental change
Baker, 2009; Chepstow- Lusty et al., 2007, 2019; Leng et al.,	Sandom et al., 2014; van Geel et al., 2003	Barnosky, ed., 2004; Damuth et al., 1992; Guthrie, 2006; Kidwell & Flessa, 1996; Shapiro et al., 2004; Western & Behrensmeyer, 2009

	Helminth eggs
	Unknown
humans	Sheep, goats, cattle, and
	Unknown
	Archaeological latrines
	Medium
surveys in archaeological contexts	Paleo- parisitological
Riera, 2011; Reinhard et al., 1986	Ejarque, Miras, &

lake sediments 2007; Schelvis, 1987, 1990, 1992

Fungi

Many fungi produce spores with thick, chitinous cell walls that presumably lend them to being well preserved in sediment records (e.g., van Geel et al., 2003; Cook et al., 2011). The thick walls of these spores likely makes dormancy possible, meaning that these spores would remain in such a state and not germinate after deposition into sediment records. A subset of these fungi utilize dung or keratin as nutrient sources, which puts them in direct association with animal hosts. Those that utilize dung (coprophilous fungi) have a well-characterized life history (Newcombe et al., 2016), including: (1) ingestion by terrestrial vertebrates; (2) defecation; (3) germination; (4) and spore ejection from the fungal fruiting bodies on the dung's surface to new substrates. If that substrate is more forage, the fungi may repeat the cycle, being ingested once more (Richardson, 2001). Spores that become incorporated into sediment records are thought to do so through short-distance wind dispersal or sticking to clayey soil particles and then washing into basins through surface runoff (Etienne et al., 2013). It has been hypothesized that the evolution of endothermy was important for the origination of coprophilous fungi, as only a few dung fungi are found on the dung of invertebrates or ectothermic vertebrates (Krug, Benny, & Keller, 2004).

The three dung fungal spore types thought to be the most reliable as PDIs are those of Podospora, Sordaria, and Sporormiella (Baker, Bhagwat, & Willis, 2013). These fungi have been applied as PDIs more than any other group. Most of these applications focus on Sporormiella because it can be relatively easily identified by its distinct gumdrop-shaped tetrad spores and sigmoid-shaped germination slits (see Fig. 1 and Bell, 2005). These applications include: documenting the rise and fall of the Inca (Chepstow-Lusty, Frogley, & Baker, 2019); dating the extinction of moas in New Zealand (Wood et al., 2011); discovering the earliest known evidence of buffalo husbandry and rice cultivation in Sumatra (Setyaningsih et al., 2019); assessing the causes of Australian Pleistocene large mammal extinctions (van der Kaars et al., 2017) and their ecological consequences (Rule et al., 2012); similarly, estimating the timing of North American Pleistocene large mammal extinctions (Halligan et al., 2016) and their ecological consequences (Barnosky et al., 2016; Gill et al., 2009; Robinson, Burney, & Burney, 2005); reconstructing pastoral landscapes (López-Merino et al., 2009; Innes & Blackford, 2003; Bowes et al., 2015; Orbay-Cerrato et al., 2017; and references therein); and investigating sediment records for the ecological consequences of historic herbivore introductions to islands (Wood et al., 2016). Other fossil dung fungal spores have been applied as PDIs too, including those of Chaetomium, Cercophora, et al, but their usefulness remains relatively unknown (Baker et al., 2013).

The usefulness of *Podospora, Sordaria, and Sporormiella* has also come under scrutiny, with recent studies questioning the fidelities of these fungi to terrestrial vertebrate dung, environmental factors affecting spore production, and sedimentary factors affecting spore preservation. Although these fungi have been referred to as obligate to dung, this is not entirely true. For example, *Sordaria fimicola* and *Sporormiella* can sexually reproduce on *Bromus tectorum* (cheatgrass) (Newcombe et al.,

2016) and may do so on other plants too. Also, *Sporormiella* can be found growing in Brazilian black and white pepper (*Piper nigrum*) (Freire, Kozakiewicz, & Paterson, 2000). This is not to say that these fungi are not indicative of dung and thus terrestrial vertebrates, but more accurately, that these fungi are commonly but not always encountered on dung. However, it is unknown how frequent these non-dung-growth cases are and how spore production from these fungi growing on substrates other than dung could be contributing to sediment records. In sum, the application of these PDIs as mostly direct substitutes for terrestrial vertebrates should be done cautiously given these alternative growth habits.

Environmental factors might also affect the utility of dung fungal spores as PDIs. These factors include how (in)tolerant dung fungi are to different climate conditions and how dung fungal communities differ between habitats. Both of these suggest that factors other than population densities (e.g., temperature, precipitation, nearby vegetation, etc.) could drive dung fungal spore quantities and mask a vertebrate population signal. For example, *Sporormiella* appears late after other dung fungi in dung fungal successional sequences (Angel & Wicklow, 1983) and is relatively tolerant of low water content (Kuthubutheen & Webster, 1986b), which occasionally may give Sporormiella a competitive advantage. However, a high water concentration may cause Sporormiella to be out-competed by other coprophilous fungi (van Asperen, 2017). This, combined with the fact that in temperate latitudes, dung fungal diversity is higher in wetter, cooler seasons and lower vice versa suggests that there may be a seasonality to dung fungal PDIs. In temperate latitudes, persistently warm and dry weather may therefore cause a lack of dung fungi, even when the terrestrial vertebrate dung that would otherwise host them is abundant. It is also known from experimental work that these dung fungi do not grow well under extreme conditions of temperature or humidity (Perrotti & van Asperen, 2019). More broadly, climate can have a significant influence on dung fungal presence and further studies are needed to address how (paleo)climate may confound interpretations of dung fungal spore assemblages as PDIs.

Significant differences in dung fungal communities between habitats can complicate the use of these fungi as PDIs too. For example, the abundance and diversity of fungal spores is much higher in peatlands than lake watersheds assumedly because these fungi are dispersal-limited and can grow directly on the peatland localities (Cook et al., 2011). This means that PDI records from peat cores could portray a much different paleoenvironmental story than those from lake sediments. Similarly, Wood & Wilmshurst (2012) found that *Sporormiella* spore abundances from cores sampled in dry habitats in New Zealand correlate well with known histories of livestock introduction and population density. However, the relationship between livestock and *Sporormiella* assemblages in wetter New Zealand habitats is less clear (Wood & Wilmshurst, 2012). Remains of testate amoebae, wetland herb pollen types, and moisture-sensitive moss spores from these wetter locations suggest that wetland soil moisture introduces a strong confounding factor for the *Sporormiella* indicator (Wood & Wilmshurst, 2012).

Spore dispersal and sedimentation are two taphonomic factors that may affect dung fungal PDI representation and utility (see taphonomic factors in Fig. 2). Regarding spore dispersal, the

spores of Sordaria and Sporormiella can be found at least 15 m above ground in meteorological samples (Haskouri et al., 2016; Hernández Trejo et al., 2012). This suggests that wind may be a more significant dung fungal spore dispersal agent than previously suggested. Also, given dung fungal PDIs take weeks to germinate and produce spores from a dung sample, defecation directly into water (e.g., from animals cooling off at a lake shore) likely contributes very few spores to these records. For ambient spores washed into these basins though, significant changes in dung fungal spore assemblages through time may be caused by changes in watershed transport and sedimentation regimes. For example, studies by Raper & Bush (2009) and Parker & Williams (2012) argued that coring proximity to shoreline is a significant predictor of Sporormiella quantities in lake sediments. Given that dung-fungal spores are thought to enter basins mostly through surface runoff, the idea here is that these spores are settling closer to shorelines than they are to deeper parts of lakes. However, a study by Etienne et al. (2013) did not find this to be a significant predictor, instead finding a significant correlation between lake inlet stream proximity and spore quantities. In all of these cases, changes in hydrologic regimes can significantly affect spore quantities by changing where the spores are deposited and how close the vertebrates in question are to a given shoreline at any given time (Fig. 2 & 3). Therefore changes in relative percentages of spores through a core should be matched carefully with sedimentary history to ensure that changes in percentages are not possibly attributable to changes in the position of inlets.

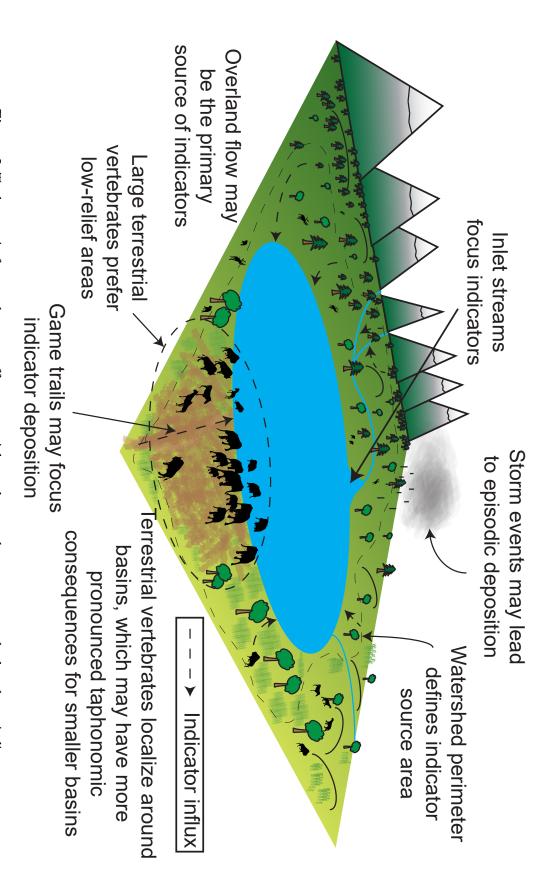
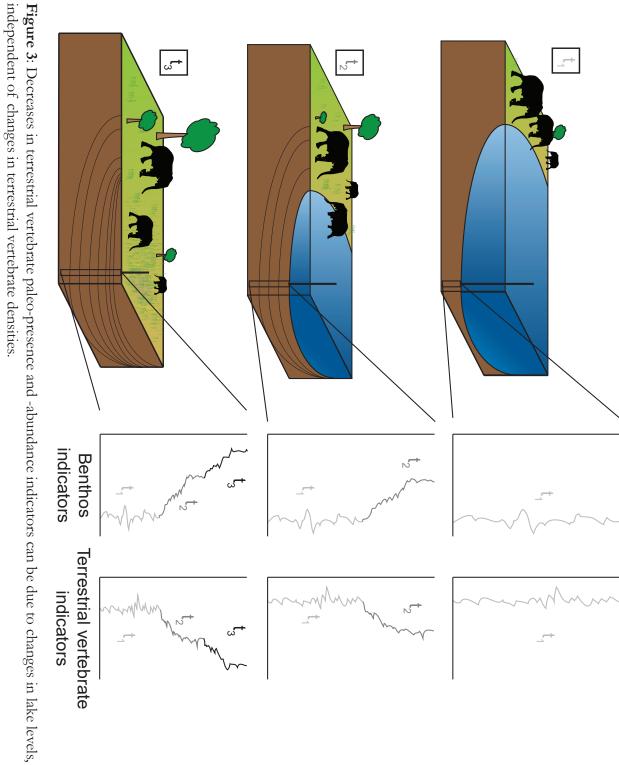


Figure 2: Taphonomic factors that may affect terrestrial vertebrate paleo-presence and -abundance indicators.



Lastly for dung fungal spores, work by van Asperen, Kirby, & Hunt (2016) showed that different palynological preparation techniques can yield significantly different spore quantities, highlighting the importance of sample processing in PDI interpretations. To account for this, Perrotti & van Asperen (2019) recommended the development of a more standardized dung fungal spore processing procedure, which would make comparisons between studies easier. This method would ideally involve minimal acetolysis to reduce spore degradation and sieving and separation by heavy liquids to maximize dung fungal spore retention (van Asperen, Kirby, & Hunt, 2016).

In summary, the factors that can significantly affect counts of dung fungal spores in cores include their fidelity to dung, their sensitivity to weather and climate, and how they are transported and deposited into sediment records. Further studies investigating how different dung fungal PDIs associate with different substrates (e.g., soils, plant tissues, different dung types) and how viable they are on each could provide insights regarding the relative importance of each substrate as a dung fungal PDI source. Actualistic studies linking temperature and humidity to dung fungal growth (e.g., Asina, Jain, & Cain, 1977; Kuthubutheen & Webster, 1986a, 1986b) in controlled lab and field settings could highlight the significance of these variables to dung fungal spore abundances, including diurnal and seasonal variability, species-specific responses to weather differences, and so forth. Tests that would be appropriate for assessing the importance of transport and deposition are highlighted below in the **Future directions** section.

Fungi that utilize keratin as a carbon source (keratinophilous fungi) have not been as well studied as coprophilous fungi, but have potential for further development as PDIs. These fungi grow on hair, nails, and skin (Lydolph et al., 2005), and their spores are presumably transported by surface runoff into depositional settings as well. Most work with keratinophilous fungi has focused on humans or archaeological sites, but a handful of studies note their incidence associated with non-human vertebrates, including mammoths, bison, horses, penguins, seals, birds, shrews, and voles (Table 1). Some of these fungi, including *Aphanoascus keratinophilous* (Cano & Guarro, 1990), *Chrysosporium tropicum*, and *C. pannicola* (Oorschot, 1980), have relatively thick spore cell walls, which might lend them to being well preserved in sediment records. However, the only evidence of keratinophilous fungi that have been associated with Pleistocene large mammals is PalEnDNA sequences of *Phialopora* and *Geomyces pannorum* (Lydolph et al., 2005).

Other fungal remains that might have potential as PDIs but have been even less studied include parasitic plant fungi recovered from dung and fungi that grow in or on vertebrate epithelial tissues. *Urocystis* is a genus of smut fungi which parasitizes many plant families. Members of this taxon may be found in cattle dung (Ejarque, Miras, & Riera, 2011) and thus through association with this terrestrial vertebrate, have potential as a PDI. The extent to which *Urocystis* and other parasitic plant fungi (e.g., *Clasterosporium caricinum, Sphaerodes*, and *Arthrinium* cf. *luzulae*) (Ejarque, Miras, & Riera, 2011) are consumed by terrestrial vertebrates and thus may be good PDIs is unknown, but is an area of future potential research. For fungi associated with vertebrate epithelial tissues—including lungs (Summerbell, 2004) and rumens (Wubah, 2004)—to become incorporated into sediment records, they need to be effectively transported outside of the vertebrate body. While it is unknown

how often this happens with fungi that grow in vertebrate lungs, the symbiotic rumen fungi *Neocallimastix, Piromyces, Orpinomyces,* and *Caecomyces* have been found as viable spores in fecal smears isolated from cattle (Wubah, 2004). The general extent to which these other fungi may be preserved as body fossils or provide PalEnDNA sequences (see below) is currently unknown.

Steroidal biomarkers

Steroidal biomarkers are organic compounds with four carbon rings that can remain unaltered in sediments for potentially millions of years (Bethell et al., 1994), making them a robust group of PDIs. Two groups of steroidal biomarkers found in sediments—5β-stannols and cholic (or bile) acids—are mostly metabolic products of digestion in vertebrates (Evershed, 1993). The 5β-stannols commonly applied include 24β-ethyl-5β-cholestano-3β-ol (5β-stigmastannol) and 5β-cholestan-3β-ol (coprostanol/coprosterol). 5β-stigmastannol is the gut-microbially-reduced form of the plant sterol sitosterol, which is derived from plant cell membranes. Because 5β-stigmastannol is only known to be formed from this pathway originating from plants, it may be an indicator obligate to plant matter or herbivore dung (Sistiaga et al., 2014). Similarly, coprostanol is the gut-microbially-reduced form of cholesterol (derived from animal cell membranes), differing from cholesterol only by a reduced double bond between C₅₋₆ (Walker, Wun, & Litsky, 1982). Coprostanol has been primarily applied as an indicator of human fecal pollution (Jeng, & Han, 1994; Müller et al., 1979; Sherwin et al., 1993; Walker, Wun, & Litsky, 1982). Coprostanol breaks down quicker in the water column than some other organic molecules (e.g., petroleum production byproducts) (LeBlanc et al., 1992) and much more quickly in aerobic conditions than anaerobic conditions (Elhmmali, Roberts, & Evershed, 1997). However, coprostanol might adsorb to sediments and become relatively stable once bound (LeBlanc et al., 1992).

The diversity of these fecal steroids is due to differences in vertebrate metabolic pathways and diets, meaning that they can be applied to identify vertebrate taxa with a relatively high degree of precision (Table 1). Some 5β -stannols can be created from microbial epimerization outside of vertebrate intestines though, meaning the presence of 5β -stannols alone does not necessarily indicate vertebrate presence (Mahaney et al., 2017). Also, the concentration of 5β -stannols in sediments can increase with input of 5α -stannols not specific to vertebrate presence, confounding the relationship between 5β -stannols and vertebrate presences. To account for this, Bethell et al. (1994) recommended normalizing the concentration of coprostanol in sediments by the abundance of total 5β - and 5α -stannols. High values of this ratio represent fresh dung, whereas values of ~ 54 -55% represent disseminated fecal input into sediments (Bethell et al., 1994). Similarly, the ratio of coprostanol to its byproduct isomer— 5β -cholestan- 3α -ol (epicoprostanol)—is known to vary between vertebrate taxa and can be used to distinguish human from marine mammal fecal inputs (Sherwin et al., 1993). A recent study by Harrault et al. (2019) demonstrated the power of these PDIs to distinguish multiple wild and domesticated Siberian mammals in an archaeological context.

They did so by comparing multiple 5β -stannols, four previously applied ratios between these 5β -stannols, and the correlation of these historic 5β -stannols with known values from recent dung samples using principal component analysis (PCA) and hierarchical clustering on principal components (HCPC). They suggest that using more 5β -stannols can resolve mammalian sources in archaeological contexts more precisely without added costs, as all of the 5β -stannols they tested can be analyzed in a single mass spectroscopy run. Although they were unable to distinguish 5β -stannol signatures from some samples using these techniques (e.g., humans and dogs with similar omnivorous diets), many taxa could be distinguished (e.g., horses from cattle, reindeer with lichen-rich winter diets vs. reindeer with lichen-poor summer diets, etc.) using these techniques. This highlights the rich potential of 5β -stannols to be further applied as PDIs.

The other group of steroidal PDIs—bile acids—are formed directly from cholesterol in the vertebrate digestive system (Evershed, 1993). They have been applied as PDIs to pinpoint the path Hannibal's army took through the Alps to invade Italy (Mahaney et al., 2017) and to document the establishment of pastoral landscapes in Southern Greenland (Guillemot et al., 2015). The primary bile acids produced in vertebrate livers are cholic acid and chodeoxycholic acid (Mahaney et al., 2017), which are then reduced by intestinal microbes into the secondary bile acids, deoxycholic acid and lithicholic acid, respectively (Evershed, 1993). After deposition, bile acids are more resistant to degradation than coprostanol (Elhmmali et al., 1997). Both primary and secondary bile acids are found in sediment records, and they are not known to be created outside of the vertebrate digestive system (Mahaney et al., 2017), making them fidelitous PDIs (Table 1). Because the concentrations of 5β-stannols and bile acids vary with digestive mechanisms (e.g., ruminants vs. monogastric mammals, herbivores vs. omnivores, etc.), the proportions of different 5β-stannols, different bile acids, and the two groups relative to each other can be very useful for differentiating terrestrial vertebrate presences from sediment records. For reference, Evershed & Bethell (1996) outline a very useful flow chart for using these proportions to distinguish human, ruminant, and porcine fecal inputs into sediments. The application of steroidal biomarkers in sediment records has been largely reserved for (zoo)archaeological and pollution studies, but holds a great potential for other vertebrates and prehistoric research.

Paleoenvironmental DNA (PalEnDNA)

Paleoenvironmental DNA (PalEnDNA) is ancient DNA (aDNA) from disseminated environmental materials (Rawlence et al., 2014). Direct sources of PalEnDNA can include bone, skin, muscle, urine, feces, eggshells, hair, teeth, gut contents, and saliva (Rawlence et al., 2014; Pedersen et al., 2015) (Fig. 1). Disseminated PalEnDNA-bearing environmental materials can include sediments, ice, soil, and tephra (Rawlence et al., 2014). Also, many reviews have focused specifically on PalEnDNA and aDNA (Rawlence et al., 2014; Parducci et al., 2017; and references therein), but few address the use of PalEnDNA as a PDI. Many terms have been applied to describe

disseminated DNA found in preserved environmental materials, including sedimentary ancient DNA (sedaDNA), dirt DNA, fossil DNA, and lake sediment DNA (lake sedDNA), but PalEnDNA succinctly and meaningfully includes all of them (Rawlence et al., 2014). As a PDI, PalEnDNA sequences have been applied to investigate the mid-Holocene extinction of the last known wooly mammoths (Mammuthus primigenius) on St. Paul Island (Graham et al., 2016) and over 5,000 years of pastoral landscape history in France (Giguet-Covex et al., 2014; Etienne et al., 2015). PalEnDNA has the distinct advantage over other PDIs for its ability to reconstruct population structures (Parducci et al., 2017), population bottlenecks (Chan, Anderson, & Hadly, 2006), and directly infer taxon-specific presences in paleoenvironments. PalEnDNA also provides a much more localized signal compared to classic indicators such as pollen and spores (Parducci et al., 2017). A more localized signal may be preferable for a given study, but should be compared with more regional signals for more synoptic paleoenvironmental reconstructions. Also, the upper age limit for which identifiable sequences of PalEnDNA can be identified is a product of temperature, pH, association with mineral surfaces, and oxygen availability (Parducci et al., 2017). Further taphonomic research on PalEnDNA—including experimental insights from modern environmental DNA—could enhance our understanding of PalEnDNA taphonomy for more informative PDI studies.

Pollen and spores

The distribution of vegetation is largely driven by climatic variables (Woodward, 1987). However, through selective browsing, trampling, and grazing (or non-grazing, in the case of *Nardus stricta* (Ejarque, Miras, & Riera, 2011)), herbivorous terrestrial vertebrates (especially ungulates) can also significantly affect and thus characterize plant communities (Gill, 2014). The scale at which this occurs can be studied in Quaternary sediment records through palynological analyses. Reconstructions of past plant communities can thus be used to infer population densities of herbivorous terrestrial vertebrates. The application of particular plant groups as PDIs can be roughly binned into two groups: pastoral pollen indicators (PPIs) and lawn grasses.

Pastoral pollen indicators (PPIs) are "a group of taxa strictly correlated to pastoral activities" (Bowes et al., 2015) (Fig. 1, Table 1). Local pastoral pollen indicators (LPPIs) are mainly entomophilous, do not disperse far from the parent plant, and are associated with pastoral landscapes through livestock disturbance regimes. These regimes include ungulate trampling/wallowing and agricultural disturbance, selective grazing, and removal or suppression of woody plants. Although they have been defined as strictly correlated to pastoral activities, the livestock behaviors that facilitate the abundances of these plants are found in modern wild terrestrial herbivores and were likely characteristic of (pre)historic wild animals too. This means that they may be found in pre-agrarian sediment records as indicative of wild, large mammalian herbivores.

Some examples of pollen types that have been applied as LPPIs include (of the Asteraceae): Aster, Centaurea nigra, Carduus, Cirsium, Matricaria, and Cichorieae (especially Cichorium intybus (Ejarque,

Miras, & Riera, 2011)); and of other groups: *Galium*-type, *Heracleum* cf., *Potentilla*, *Ranunculus*, and Ranunculaceae. An important taphonomic note for LPPIs is that substrate type and landscape openness independent of large herbivore behaviors can also correlate with the presence of LPPIs (Ejarque, Miras, & Riera, 2011), obscuring their fidelity as PDIs.

Regional pastoral pollen indicators (RPPIs) are also indicative of pastoral landscapes and thus grazing terrestrial vertebrates, but are dispersed more widely. These include pollen grains from *Artemisia*, Chenopodiaceae, *Plantago lanceolata*, and *Plantago major/media* (Mazier et al., 2006). Because these taxa are also anemophilous (see Clifford, 1962; Tkach et al., 2007; Borsch, 2009), their wider dispersal makes sense. As implied above, some of these pastoral indicators have also been verified as indicators of wild grazing ungulates, and it is often difficult to distinguish the effects of wild vs. domesticated grazers from pollen records. For example, the increased abundance of *Plantago lanceolata* before the Holocene elm decline in the English Lake District might have been caused grazing deer (Buckland & Edwards, 1984).

For some PPIs, it is unknown the extent to which they are more local vs. regional PDIs. These include *Urtica dioica* (stinging nettle) (López-Merino et al., 2009; Ejarque, Miras, & Riera, 2011), *Polygonum aviculare*, and Cerastium-type (Schofield & Edwards, 2011), and *Rumex* (Mazier et al., 2006). *Rumex*, however, is often found on the margins of wetlands, is only sporadically recovered from pastoral sites, and is thus not a reliable PPI (Mazier et al., 2006). Similarly, Cichorieae pollen types are commonly reported as LPPIs, but can be more commonly associated with Mediterranean river bed vegetation than pastoral landscapes (Florenzano et al., 2015), meaning that their fidelity to grazing terrestrial vertebrates is questionable. For pastoral landscapes, artificial mowing can result in pollen assemblages similar to those resulting from grazing behaviors, and it can thus be difficult to distinguish the two causes from a pollen assemblage alone. For example, *Ramunculus acris*, *Plantago lanceolata*, Cichorioideae, and Poaceae can be found in both artificially mown and naturally grazed landscapes (Hjelle, 1999). Also, Poaceae can include grasses that are more indicative of wetlands—such as reeds (e.g., *Phragmites*)—than grazing activities.

Some non-ruderal plants, including Scrophulariaceae, *Linaria*-type, *Sedum*, and Cyperaceae have been observed in livestock feces (Ejarque, Miras, & Riera, 2011) and thus might be valuable as PDIs. In areas where grasses were not present before human arrival, Poaceae can act as a livestock indicator (Ledger, Edwards, & Schofield, 2014), but this limited application is thus reserved for pastoral applications and is likely not meaningfully applicable as a PDI for wild vertebrates. Similarly, many of these pastoral plants can be found in human-disturbed habitats, independent of other terrestrial vertebrate activities. The degree to which these pastoral plants have recently become adapted to human- vs. herbivore-disturbed habitats is unknown, but may limit our ability to test the associations between these PDIs and actual terrestrial vertebrate population densities using modern studies. An interesting behavioral consideration that Hjelle (1999) observed is that some of these pastoral plants are grazed before flowering. These plants may be indicative of grazing behavior, but because their pollen dispersal can be suppressed by grazing, they might be underrepresented in pollen assemblages.

Along with PPIs, lawn grass taxa may also produce fossil assemblages indicative of terrestrial vertebrates. Lawn grass taxa are short statured plants that are grazing-adapted (Archibald et al., 2005). In areas of intense grazing such as the African savanna, lawn grass taxa can be found in abundance as grazing lawns—expanses of short grasses actively created and maintained by grazing (J.T. Verweij et al., 2006). Grazing lawns can also be found in western Alaska as swaths of Carex subspathacea (a sedge, not a grass) created by grazing black Brant geese (Branta bernicula nigricans) (Person et al., 2003). Carex subspathacea is an important indicator because it is only found in grazing lawn form, making it an obligate indicator of goose behavior and highlights the fact that large ungulates are not the only animals that can make grazing lawns. In general, these lawns can range from a few square meters to square kilometers, depending on the herbivores present, herbivore population densities, and landscape structure (Person et al., 2003). For example, hippos (Hippopotamus amphibius) and kob (Kobus kob) are known to maintain grazing lawns in different locations from each other (J.T. Verweij et al., 2006). It is important to note that swards, or expanses of even-statured (mostly defined as short-statured) grasses, can be also be classified as grazing lawns and include lawn grass taxa, but are not necessarily created by grazing. Likewise, some grazing lawns are facultatively created, but obligate lawns with plants that require regular grazing hold the highest potential as PDIs. Obligate grazing lawn plants from Africa are the best studied, and include the grasses Andropogon greenwayii, Cynodon dactylon, C. plectostachys, Paspalum conjugatum, Pennisetum clandestinum, and Stenotaphrum secundatum. (Hempson et al., 2015).

A major consideration for utilizing lawn grasses as PDIs is that they produce pollen grains that are visually distinct and preserve well. Distinguishing different grasses in pollen assemblages is notoriously difficult, but these lawn grasses may also produce distinct phytoliths that preserve well and could thus be utilized as PDIs. No known studies have yet actively sought to link pollen or phytolith assemblages with grazing lawns in sediment records, so this remains a potential area of further research. For pollen PDIs, the ability of fire to open landscapes and promote plants that favor open landscapes may produce pollen assemblages indistinguishable from those produced by terrestrial vertebrate herbivores. For example, *Pteridium aquilinum* and *Melampyrum* have been suggested as grazed forest indicators, but may also benefit from fires (Svenning, 2002). Also, significant changes in browse-plant quantities inferred from their pollen types could indicate changes in terrestrial vertebrate paleo-population densities. For example, an increase in the abundance of *Fraxinus nigra*-type and *Ostrya/Carpinus* pollen from Appleman Lake, Indiana, at 13.7 ka is thought to be from a loss of Pleistocene megaherbivores (Gill et al., 2009). Similarly, the spread of *Nothofagus* forests in southwestern Patagonia may have resulted from the loss of Pleistocene megaherbivores there (Barnosky et al., 2016).

Fossil bones

Extrapolating population densities of large mammals from fossil bone records is well known to be a questionable task (Bradshaw, Hannon, & Lister, 2003). Large-mammal bones tend to have wider distributions in space and time about a given environment; however, fossils of small mammals can be more localized in space and can provide valuable information on small-mammal population densities (Hadly, 1994; Barnosky, 2004; Terry, 2008). Some studies have attempted to utilize temporal clusters of radiocarbon dates from bones of large mammals as indicators of population density. The idea here is that if there are many vertebrates leaving their radiocarbon-datable bones on landscapes, we can infer from clusters of these dates that there were many individuals at that location at that time and that changes in these clusters may represent changes in population densities. For example, Pleistocene-Holocene radiocarbon date clusters of horse, wooly mammoth, bison, wapiti, moose, and human bones have been used to investigate the timing of large mammalian herbivore extirpation vs. human arrival in Siberia, Beringia, and northwest North America (Alaska and the Yukon Territory) (Guthrie, 2006; Zimov, Zimov, & Chapin, 2012). In a more sophisticated approach, Steele (2010) investigated the record of North American human radiocarbon dates to estimate initial Pleistocene-Holocene colonization speeds. By binning frequencies of radiocarbon first-appearance data (FADs) for humans in North America, Steele (2010) argued that this event frequency could be used as a proxy for population concentrations. Similarly, Goldberg, Mychajliw, & Hadly (2016) estimated the population density of South American humans throughout the Holocene by utilizing Bayesian- and likelihood-based models applied to radiocarbon FADs.

Although I include radiocarbon date clustering as a PDI, these studies have actually attempted to determine the spatial distributions of FADs and last-appearance dates (LADs). In general, clustering radiometric dates of bones to infer paleo-population densities is a very rough approach that involves a relatively high degree of time-averaging and has only been applied at regional scales. It may, however, provide insights regarding at least the presence and possibly the relative abundances of vertebrates through time. By applying this approach to more localized scales at localities with high-resolution vertebrate chronologies (e.g., select bone assemblages in caves), a closer sense of population density might be achievable.

Invertebrate remains

Some invertebrates are well-known to be associated with terrestrial vertebrates and have hard parts that preserve well. These include select dung beetles (Coleoptera: Scaraboidea in the families Geotrupidae, Aphodiinae and Scarabaeinae) (Raine & Slade, 2019), oribatid and gamasid mites (Class: Arachnida, Order: Oribatida; Order: Parasitiformes), and helminth (parasitic worm) eggs. Dung beetles in particular are intuitively associated with terrestrial vertebrates through

vertebrate dung. The chitinous remains of dung beetles can be found in archaeological deposits (van Geel et al., 2003), woodlands, pastures (Sandom et al., 2014), and tar pits and tar seeps (Miller, 1983) (Table 1). Although no studies have yet applied dung beetle assemblages to explicitly infer vertebrate paleo-population densities, their remains have been applied to argue that the loss of late-Pleistocene large mammals caused a decrease in dung beetle diversity in Great Britain (Sandom et al., 2014) and a downsizing of dung beetles throughout Europe (Schweiger & Svenning, 2018). Notably, dung beetle body size is well-known to be closely correlated to dung size, which in turn is closely related to dung-producer size (Hanski & Cambefort, 2014). Although this is not quite taxon-specific, it may mean that mean that the sizes of dung beetle remains in paleo-records could be used to infer the presences of some vertebrates over others (e.g., large dung beetles associated with proboscidean dung vs. smaller dung beetles associated with antelope dung). Some limitations behind applying dung beetle remains as PDIs include the fact that dung beetle macrofossils are better preserved in wet areas (Sandom et al., 2014) and their remains cannot be temporally resolved as well as microfossil PDIs can. Also, dung beetles can become associated with other hosts or become frugivorous if their dung-producing hosts disappear, as may have happened as part of the late-Quaternary extinction event (Raine & Slade, 2019). Thus, if dung beetles are to be applied as PDIs, they should be done so in conjunction with paleo-hydrological indicators (e.g., remains of diatoms, chironomids, testate amoebae) and other PDIs for comparison.

Regarding mites, the two groups that may be the most useful as PDIs are oribatids and gamasids. Oribatids are small (~1 mm), generally soil-dwelling detritivores that can be found in moist habitats on decaying vegetation, soil, and dung (Chepstow-Lusty et al., 2007). Most oribatids have a low dispersal ability (Gulvik, 2007) which may make them useful for inferring local terrestrial vertebrate paleo-population densities. They have been applied mostly as indicators of local plant communities and habitats (e.g., peat bogs vs. oligotrophic lakes) (Solhøy, 2001), but a few studies have focused on select taxa as dung, pasture, and large herbivore indicators (e.g., Baker, 2009; Chepstow-Lusty et al., 2007; and Schelvis, 1992). Studies by Chepstow-Lusty et al. (2007, 2019) are the only ones that have focused on these mites as indicators of vertebrate densities in a stratigraphic context, which highlights the untapped potential for further research.

Like oribatids, gamasids are generally characteristic of environments rich in decaying organic matter and have been found in deposits consisting almost entirely of human and animal feces. However, historic remains of mites can be difficult to identify because their diagnostic legs, genitalia, and other features do not preserve well (Schelvis, 1990). One benefit of working with mites as PDIs though is that mite researchers have compiled detailed tables of associations between mite taxa and vertebrate dung. For example, Table 1 from Baker (2009) has information on a diverse set of mites from coprolites from Brazil and the US, and a publication by Schelvis (1992) has multiple tables with associations between gamasids and host dung samples. Again, these tend to be focused on domesticated animals for zooarchaeological purposes, but there is the potential for non-domesticates as well.

Lastly for invertebrate PDIs, parasitic worm (helminth) eggs are commonly found in fresh dung samples and coprolites (e.g., Reinhard et al., 1986, Ejarque, Miras, & Riera, 2011). These eggs are $\sim 100 \, \mu m$ long and ovoid with grainy textures (see Fig. 1). They are very resistant to decay, having multiple layers that resist desiccation, strong acids and bases, oxidation, reduction, detergents, and proteolytic compounds (Jimenez, 2007, Fairweather & Threadgold, 1981; Quilès, Balandier, & Capizzi-Banas, 2006). Reinhard et al. (1986) reported their abundances in a stratified medieval latrine, suggesting that they may be found in other stratigraphic contexts too. Ejarque, Miras, & Riera (2011) reported that helminth egg abundances in modern domesticated livestock feces are higher than those for non-domesticates, suggesting a degree of taxonomic specificity. For their use as archaeological indicators and by extension, PDIs, the eggs of Ascaridae, Capillaridae, Trichuridae (whiptail worms), Oxyuridae, and cestodes (e.g., tapeworms) have been proposed as particularly useful (Bouchet et al., 2003). Other helminth eggs—including those from Hymenolepsis, Dicrocoelium dentriiicum, and Enterobius vermicularis—have also been found in stratified archaeological contexts but their potential utility as PDIs is less known, especially for other contexts (e.g., lake and peat sediments, cave records, etc.). Also, although helminth eggs are relatively resistant to decay, they are still subject to taphonomic alteration, including fracturing possibly from frost wedging (Reinhard et al., 1986). Plus, while some archaeological sites have well-preserved helminth eggs, other sites with similar climates have poorly preserved or absent eggs for reasons unknown.

Given these eggs are commonly found in bulk sediments, some paleo-parasitologists have attempted to isolate them using palynological processing techniques, including acetolysis and separation by density (Reinhard et al., 1986). These methods are favorable because the eggs that survive this process are cleaned by it and are thus easier to identify. In general though, helminth egg identification is notoriously difficult. For example, some diagnostic features may be obscured by using density separation techniques, and some eggs can be commonly confused with fungal spores. Also, with density separation, many techniques have been proposed, but there is currently no 'catch-all' standard approach that works for most helminth eggs from most sites.

Other indicators

Lastly, δ^{15} N values and remains of aquatic macroinvertebrates may have potential as unexplored PDIs. Work by Foote and Hornung (2005) showed that dragonfly and damselfly (Order: Odonata) diversity and abundance negatively correlates with cattle grazing pressure in Alberta, Canada. If bodily remains or PalEnDNA sequences from these insects preserve well in aquatic sediments, they may have potential as PDIs. Also, Keatley et al. (2011) argued that δ^{15} N values in a lake sediment core profile closely matched the proximity of seabird colonies, as seabird nitrogenous wastes are δ^{15} N-enriched relative to terrestrial and freshwater sources.

General taphonomic considerations

Given all of these remains are indicators and not quite proxies, their absences in sediment records may not necessarily reflect actual terrestrial vertebrate absences and vice versa. Davis (1987) exemplified this in the case of livestock being present around ponds when *Sporormiella* was absent from those pond sediment records. In general, this calls for further taphonomic consideration and testing, including more actualistic experiments, studies of vertebrate behaviors regarding PDIs, research comparing PDI sedimentation with actual population density records, refined PDI identification methods, and improved analytical methods.

Actualistic experiments

The taphonomic uncertainties associated with these indicators all call for actualistic experiments to assess the effects of environmental factors on PDI quantities. However, while existing actualistic studies note the importance of modern factors affecting PDI quantities (e.g., temperature and humidity affecting dung fungal growth), it is largely unknown the extent to which these modern environmental determinants are 'washed out' as noise in sediment records. This is not to say that these studies are uninformative, but that it is difficult to determine *a priori* which modern factors are most important for PDI taphonomy. Particularly informative experiments could involve known terrestrial vertebrate population densities in defined areas such as zoos, reserves, and sanctuaries. For example, an exceptional study by Baker et al. (2016) compared population records of vertebrates at a preserve in The Netherlands around human-made ponds ~16-31 years old with influx/accumulation rates of dung fungal spores. This study showed a significant correlation between the population densities of these vertebrates and dung fungal spore influx/accumulation rates retrieved from the pond sediment records. More studies that have similar time-spans should be conducted to bridge known terrestrial vertebrate population densities with resultant PDI quantities in recent sediment records.

Vertebrate behaviors and representation in sediment records

Given that vertebrates are known to concentrate around watering holes (Deocampo, 2002) and defecate in select latrines regularly (Perrotti & van Asperen, 2019), these behaviors may result in localized hotspots of PDIs (Fig. 2). Also, some vertebrates may have migratory behaviors that lend them to only being occasionally present around a given depositional site (Fig. 2). In a sediment record with a high temporal resolution (e.g., varved lake sediments), this may be observable as a seasonal trend. However, with a given hydrologic regime during the season of vertebrate presence, select PDIs may not preserve well and could thus represent a false extirpation event. Lastly, some

dung-loving arthropods (e.g., dung beetles, dung fungal gnats, etc.) can be significant dung fungal spore dispersal agents, which may lead to spores being dispersed much further away from their vertebrate hosts than expected (Graf & Chmura, 2006). The extent to which this could affect dung fungal spore records is unknown.

Sedimentation vs. actual paleo-population density

As previously mentioned for dung fungal spores, the causes for changes in PDI quantities may be difficult to distinguish (Dodson & Field, 2018) (Fig. 3). These could include changing shoreline conditions, episodic deposition (e.g., storm events), and dispersal from the vertebrate source to the coring location (Fig. 2 & 3). This is a potential concern for all other indicators mentioned (except radiometric date clustering) as well.

In general, the relationship between mesic vs. xeric conditions and microfossil PDI sedimentation and preservation is unclear. Overland flow of these indicators may lead to increased influx/accumulation rates, but for a given coring site, a laterally-expanding lake margin would mean that these indicators are settling out of the water column further away from the coring site (opposite from Fig. 3). Alternatively, a storm event could cause increased runoff of PDIs into a basin, dispersing PDIs into areas they would not normally reach (Cook, 2009) (Fig. 2). This could be inaccurately inferred as an acute terrestrial vertebrate population density growth event. Also, the grain size of the surrounding sediment is known to be a significant determinant of spore concentrations (Holmes, 1994) and thus may be so for microfossil PDIs as well. For example, sandy layers in a sediment core may represent high-energy times where significantly smaller microfossil PDIs might have been washed away and thus not preserved. Relatedly, as mentioned above for fungal spores sticking to clayey particles, a lack of clay minerals may result in lower preservation rates of microfossil and molecular PDIs, as they would have less sticky sediment to adhere to.

The shape of a lake basin may also affect the relationship between sedimentation and actual terrestrial vertebrate population density. For example, there may be plenty of vertebrates around hypothetical pan lakes/playas, but given the shallow nature of these lakes, the PDIs would likely be eroded and not well preserved. There may also be plenty of vertebrates around low-altitude and steeply-deepening rift lakes, but given the relatively low sediment influx/accumulation rates of those lakes, the preservation potentials there may be sub-optimal to compare low-resolution PDI quantities with paleo-population densities. The bowl-like shapes of alpine lakes may be ideal for preserving PDIs, but large vertebrates may avoid high-altitude locations to conserve energy (Taylor, Caldwell, & Rowntree, 1972; Wall, Douglas-Hamilton, & Vollrath, 2006). With those considerations, kettle and impact crater lakes are likely the best depositional environments for both focusing terrestrial vertebrates and reducing the chance that PDIs will be eroded or bioturbated.

PDI identification difficulty

As previously mentioned for dung fungal spores and helminth eggs, microfossil identification can be notoriously difficult. A trained eye in microfossil identification may take years to acquire, and even then, some microfossil groups are notoriously difficult to differentiate yet are ecologically distinct and important as indicators. This can limit the ability of researchers to apply PDIs for more comprehensive paleoecological studies, as the utility of many microfossil indicators is limited by their ability to be taxonomically resolved. The ability to more precisely and completely identify microfossil indicators would allow for microfossil-vertebrate associations to be more thoroughly and rigorously applied towards questions of how specific vertebrates interact with landscapes through time. Similarly, the vertebrate taxonomic resolution available with these indicators is quite variable and dependent upon multiple factors. These factors include the ability to identify microfossils to the species-level, the preservation and quality of PalEnDNA sequences, and the relative fidelities between PDIs and their vertebrate sources. Each of these concerns should be addressed to more precisely understand the relationships between terrestrial vertebrates and their paleo-environments through time.

Analytical concerns

For quantifying microfossil PDIs, the pros and cons of using relative quantification/abundance (microfossil quantity as a proportion of a total microfossil sum), concentration (microfossils per unit mass or volume), and influx/accumulation rate (microfossils per unit time and catchment area) have been addressed in detail by Baker et al. (2013) and Perrotti & van Asperen (2019). Both of these studies recommend using accumulation/influx rates as the most accurate way to quantify microfossil PDIs. Also, inferring changes in PDI quantities is often not done in a statistically significant manner. This is a problem because visual differences may not be analytically or paleoecologically meaningful. Statistical change-point analyses for univariate time series—including break or "two-phase" regression, Bayesian, and likelihood approaches—are particularly informative for identifying significant changes across temporal scales in climatological time series (Mudelsee, 2014a) and may also be particularly useful for PDI studies. These change-point detection methods are currently under-developed within the paleo-sciences in general (Mudelsee, 2014a), but could be advanced with insights from the statistical literature.

Future directions

There are many potential directions that could be taken to advance PDIs, including improving the understanding of relationships between PDIs and climatic factors, understanding

transport into lacustrine settings, comparing indicators together, streamlining identification techniques, extracting PalEnDNA from the indicators themselves, and applying PDIs to pre-Quaternary records.

Understanding climatic influences on PDIs

As previously mentioned for dung fungal spores, weather and climate are known to directly affect PDI quantities. These factors likely affect other fungal PDIs and invertebrate PDIs, and are known to affect pollen PDI quantities. Weather and climate can also indirectly affect PDI quantities through hydrogeologic processes, including pulses into depositional basins from storm events (Fig. 2). For dung-based PDIs especially, environments that are too wet may cause the dung to wash away or become too runny before significant PDI inhabitation can occur (e.g., dung fungal growth, dung mite and beetle occupation, etc.). As mentioned above, cultivating these indicators under controlled lab and field conditions can elucidate our understanding of these factors. For example, experimental work showing how dung fungal spore production rates vary between treatments of temperature and humidity on shorter time scales (e.g., diurnal temperature fluctuations, artificial rainfall events, etc.) could aid our understanding of how these acute factors could affect dung-based PDI production. At longer time scales, field-based experiments in locations with variable temperatures, humidities, wind velocities, vegetation, physiographic conditions, etc. could help aid our understanding of how these broader environmental factors affect dung-based PDI production. This could be especially insightful for understanding situations where large mammalian herbivores are known to be present but recent sediment records do not capture PDIs to corroborate this.

Understanding transport mechanisms into lacustrine settings

As Figures 2 & 3 show, the pathway a PDI may take from a vertebrate to a lacustrine basin can be complicated by many factors. These hydrogeologic complications can obscure the relationship between population densities and PDI quantities. Thus, understanding how these processes affect these relationships can bring us closer to accurately inferring population densities. Ideally, a long-term study to get at these factors could involve an experimental lake basin with known terrestrial vertebrate population densities and terrestrial (e.g., Tauber, 1974) and aquatic sediment traps to compare population densities with PDI influx/accumulation rates over many years. Physiographic factors of a given watershed—including relief, slope, aspect, and game trails—could be accounted for in this study to determine their contributions to PDI sediment records. Also, flume-based studies could improve our understanding of PDI microfossil sedimentology, which could provide insights regarding associations between PDI quantities and changes in hydrogeologic regimes.

Comparing indicators together

To investigate the effects of other environmental variables on PDI quantities, other indicators should be included in the same studies. This is especially important because some PDIs can mismatch even in the same record, suggesting that at least one of them is not accurately representing population density. For example, Chepstow-Lusty (2019) found that quantities of Sporormiella and Oribatid remains did not correlate with each other, even when the study area was known to have thousands of camelids present at times. Also, many researchers interested in timing Quaternary megafaunal extinctions using radiocarbon LADs and Sporormiella have found discrepancies between Sporormiella declines and the most recent Pleistocene megafaunal radiocarbon dates. For example, Gill et al. (2009) found Sporormiella to decline ~1,000-2,000 years before Pleistocene megafaunal LADs determined from radiocarbon samples. As Sporormiella is thought to be a higher-resolution microfossil indicator of large herbivore population densities, Gill et al. (2009) suggested that this discrepancy represents an initial population decline inferred from the Sporomiella, and a final population crash inferred from the radiocarbon dates. However, the opposite pattern could hold true in other cases, where LADs from bone records could preceed Sporormiella declines due to a low bone preservation potential in a given region or landscape. For paleoenvironmental indicators other than PDIs, remains of diatoms, chironomids, and testate amoebae can act as paleo-water-level indicators, which could control for the effects of basin size changes on PDI quantities. Similarly, quantities of Glomus—an endomycorrhizal fungus that forms spores below the soil surface (Cook et al., 2011)—and x-ray fluorescence (XRF) measurements could be used to detect changes in erosional regimes through time.

Different PDIs should be investigated in conjunction to test for covariances between two or more PDIs. If the covariances between two or more PDIs match (i.e., they correlate) and if these covariances match potentially known population density values, this suggests that these PDIs accurately represent population densities. If the covariances between two or more PDIs do not match each other or potentially known population density values, this would suggest that there are taphonomic/fidelity concerns that are hindering the usefulness of one or more of these PDIs. Spearman's grade correlation coefficient (*r*s)—a form of Spearman's rank correlation coefficient (*Q*s) modified for continuous random bivariate distributions (Mudelsee, 2014b)—may be an appropriate metric for testing the correlation between two PDI series.

Methods to improve microfossil PDI identification

A growing number of microfossil morphotypes have been photographed and cataloged (Doyen & Etienne, 2017). If microfossil morphotypes can be identified through machine learning, this may ameliorate the time spent trying to identify morphotypes and the expertise required to do so. This may be especially helpful for distinguishing different species of coprophilous fungi, who

differ only by slight variations in their spore axis lengths (Bell, 2005). As different species of coprophilous fungi have different host dung preferences, this may open the door to accurately making more refined spore-host association claims with microfossils (Baker, Bhagwat, & Willis, 2013).

PalEnDNA of indicators

Although indirect compared to genetic sequences directly from focal vertebrates, all of the aforementioned indicators (except steroidal biomarkers and nitrogen values) are sources of PalEnDNA too. As with above, correlations between PDIs, PalEnDNA from focal vertebrates, and PalEnDNA from PDIs could highlight taphonomic discrepancies relating to DNA transport and preservation. This may be currently infeasible, however, given the difficulty behind extracting miniscule quantities of vertebrate PalEnDNA, let alone the PalEnDNA of PDIs.

Pre-Quaternary applications

Except for PalEnDNA which has yet to be preserved from pre-Quaternary sediments and radiocarbon date clustering which does not work for pre-Quaternary records, all of the aforementioned PDIs were likely present in pre-Quaternary depositional environments too. Thus, these indicators should be observable in pre-Quaternary sediments as well. For example, *Sporormiella* has been found in Pliocene (Andreev et al., 2014) and even ~11.5 million-year-old Miocene sediments (Davis & Ellis, 2010). Also, dung beetles might have originated with mid-Cretaceous angiosperms and would thus have been associated with large herbivorous dinosaurs, but are at least associated with Paleogene megafauna (Schweiger & Svenning, 2018). And similarly, if the life cycle of dung fungi mostly centers around large terrestrial herbivores, spores of these fungi may be present in Paleogene sediments—possibly indicative of the first large mammals. By further exploring Quaternary and pre-Quaternary sediment records for PDIs, we may be able to gain novel insights regarding the paleoecology of terrestrial vertebrates and their environments through time.

Chapter 2: Chronology of late Quaternary megafaunal extinction, paleoenvironmental change, and human arrival in Brazil

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Abstract

Much work has investigated the late-Quaternary extinction event at continental scales, but few studies have focused on regional scales. I sought to investigate the vertebrate paleontological, archaeological, vegetational, and climatic conditions surrounding the late-Quaternary extinction event in Brazil, an area of South America that had not previously been studied in such detail. To do so, I utilized pre-existing references for all known Brazilian Pleistocene archaeological and megafaunal radiocarbon dates, and used the distribution of the resulting 1,163 archaeological dates and 13 megafaunal dates to estimate the arrival and humans and extirpation of megafauna. These arrival and extirpation estimates were compared with nearby paleoclimate and paleovegetation records. For Brazil as a whole, I calculated a megafaunal extirpation age estimate of 12,656-11,696 Cal yr BP and a human arrival age estimate of 22,893-16,005 Cal yr BP. I found that humans, climate, and vegetation change correlate with Brazilian Pleistocene megafaunal extirpation, in the form of gradual human population growth, regional effective moisture changes, and regional vegetation change. This highlights the need for finer regional studies to investigate the chronologies of these events for synthetic comparisons between regions of Brazil.

Keywords

Brazil, Extinction, Quaternary, Megafauna, Paleoenvironment, GRIWM

Introduction

Over the past 50,000 years, about half the world's large mammal species have become extinct from a combination of human population pressures, climate change, and habitat loss (Brook

& Barnosky, 2012). These late-Quaternary extinctions (LQE) peaked around the end-Pleistocene, which was an age of significant global environmental change, including human population expansion, warming following the last glacial maximum (LGM; ~24-18 ka) (Clark et al., 2009), a brief cold snap during the Younger Dryas (~12.9-11.7 ka) (Fairbanks, 1989), and regional biome reconfigurations (Williams et al., 2004). All of these changes resembled ongoing and projected global changes, although they were of much lower magnitude and velocity. Nevertheless, the resemblance in the kinds of potential forcing factors of extinction makes understanding the LQE especially important for understanding the modern biodiversity crisis.

The causes of the LQE have been intensely debated for decades and have focused on anthropogenic vs. climatic mechanisms (Wroe, 2004; Koch & Barnosky, 2006; Bartlett et al., 2016; Araujo et al., 2017; Monjeau et al., 2017; Nagaoka, Rick, & Wolverton, 2018). Additionally, recent work has focused on the ecological consequences of the LQE (Johnson, 2009; Blois, McGuire, & Hadly, 2010; Gill, 2014; Pires et al., 2014, 2015, 2018; Smith et al., 2016; Galetti et al., 2018; DeSantis et al., 2019), which is shedding new light on the environmental changes and potential feedbacks that accompanied the extinction event. Identifying these consequences hinges upon whether habitat changes preceded or followed the LQE, which requires a robust chronology of the paleoenvironmental conditions surrounding the LQE. This is difficult to establish because the LQE was time-transgressive on a global scale and spread over thousands of years between continents. Most previous work has focused on these continental scales, but as both the amount of dated materials and precision in radiocarbon dating have increased, workers are becoming more able to discover intricacies between regions, taxa affected, and specific paleoenvironmental conditions surrounding the megafaunal losses.

A region of particular interest is Brazil, given that previous work has shown that at a continental scale, the LQE was the most severe in South America, with over 50 megafauna genera (~83%) seeing extinction (Koch & Barnosky, 2006; Borrero, 2009; Hubbe, Hubbe, & Neves, 2013; Martin & Borrero, 2017; Polotis et al., 2019). Lost forever were giant ground sloths (Mylodontidae, Megatheriidae), car-sized armadillos (Glyptodontidae), the rhino-like toxodons (Toxodontidae), and a proboscidean (*Notiomastodon platensis*). Other studies have highlighted regional trends for other parts of South America (e.g., Barnosky et al., 2016; Villavicencio et al., 2015), but the Brazilian paleoenvironmental record surrounding the LQE has yet to be similarly investigated. To more thoroughly investigate this record in relation to the LQE in Brazil, it is necessary to establish a refined, high-precision chronology of: 1) when humans first arrived; 2) how vegetation was changing around this time; 3) how climate was changing; and 4) how the chronologies of these events align with megafaunal extirpation.

To investigate this, I compiled a list of published radiocarbon dates for extinct Quaternary megafauna and archaeological sites in Brazil, estimated human arrival and megafaunal extirpation dates using the Gaussian resampled inversely-weighted McInerny et al. method (GRIWM) (Saltre et al., 2015), and compared the estimated arrival and extirpation dates to published paleo-vegetation and -climate records. The data were used to investigate four alternative working hypotheses:

1) Megafauna loss caused an ecological "ripple effect" on vegetation (i.e., a defaunation signal from changes in herbivory and/or seed dispersal) (e.g., Dirzo et al., 2014; Barnosky et al., 2016; Ripple et al., 2015; Young et al., 2016). Rejecting this hypothesis would require that the decline of megafauna postdated certain kinds of vegetation shifts.

- 2) Loss of habitat was a chief cause of megafauna extinction. Rejection requires that vegetation shifts occur before the megafaunal decline.
- 3) Climate change was the ultimate driver of megafaunal decline, possibly mediated through changes in the plant communities. If vegetation shifts and megafauna declines were concurrent and matched a pronounced paleoclimatological change, this would be consistent with climate change being the ultimate driver of extirpation. Rejecting this hypothesis would require a significant mismatch in the timing of climate change, vegetation change, and megafaunal loss.
- 4) Human pressures—direct, indirect, or a combination of both—were the chief driver of megafauna loss. If certain vegetation shifts (e.g., those consistent with aboriginal land management with fire and/or landscape modification for favored vegetation) and megafauna decline was concurrent but do not match a pronounced paleoclimatological change, this would be consistent with human population pressures causing both the extirpation and vegetation change. This hypothesis could be rejected if the nature of vegetation change was not consistent with aboriginal land-management practices, or if it could be demonstrated that human entry into the area or an increase in their population sizes did not coincide with the megafaunal decline and vegetation change.

(Paleo) climate of Brazil

Brazil is a large country with a heterogeneous climate, but generally is characterized as humid around the equator and along the Atlantic coast, and drier further south and inland. Over broad spatial scales, the intertropical convergence zone (ITCZ) and South American summer monsoon (SASM) are important climatic factors. The ITCZ is a band of high precipitation and temperatures spatially defined by the annual north-south migration of the meteoric equator about the geographic equator (Garrison, 2012). Ranging annually from 10° N in August to 1° S in March (Baker & Fritz, 2015), the ITCZ thus affects broad spatiotemporal climate patterns in tropical Brazil. The South American summer monsoon (SASM) brings significant moisture from the Atlantic Ocean to southeastern Brazil during the austral summer months (Cruz et al., 2005), whereas the ITCZ deposits rainfall further north. Also, although El Niño / Southern Oscillation (ENSO) is an important climatic factor for other South American regions, there is little support for it to explain modern and historical high amplitude, low frequency precipitation events in Brazil (Baker & Fritz, 2015). The ITCZ and SASM, however, have affected Brazil's climate throughout the Quaternary—even with changes in insolation—and were likely affected by end-Pleistocene global climatic events as well.

Paleoclimatically, both local and large-scale events are discernable from Brazil's prehistoric records, including relatively wet conditions in southeastern Brazil during the LGM and dry conditions in the early- to mid-Holocene (Baker & Fritz, 2015). Aside from a lake (Moro et al., 2004) and peat (Ledru et al., 2005) sediment record from southern Brazil and two marine sediment core records from northeastern Brazil (Nace et al., 2014), speleothem records from southeastern Brazil (e.g., Cruz Jr. et al., 2005; 2006)—especially those from Botuverá Cave—are the main paleoclimate archives for the country. All of these records suggest that precipitation response to climate change was not uniform across regions of Brazil. For example, southern Brazil became drier after the LGM,

then wetter at the start of the Holocene, followed by drying and several more effective moisture oscillations during the rest of the Holocene (Moro et al., 2004). Conversely, northeastern Brazil became wetter after the LGM, followed by a sharp decrease in effective moisture ~14-14.5 ka, then a sharp increase in effective moisture ~14-12 ka, and finally gradual drying throughout the Holocene (Nace et al., 2014). These differences highlight how paleoclimatic changes in Brazil cannot be generalized for the entire country and must be examined by region to understand their effects on Brazilian Pleistocene megafauna.

Bioregions of Brazil

As directly affected by Brazil's climate, Brazil's vegetation can be categorized into seven distinct bioregions with ecotones between them: the Pampas, the *Araucaria* Plateaus, the Atlantic Rainforest, the Pantanal, the Amazon Rainforest, the Cerrado, and the Caatinga (see Figs 4 and 5 for overview maps).

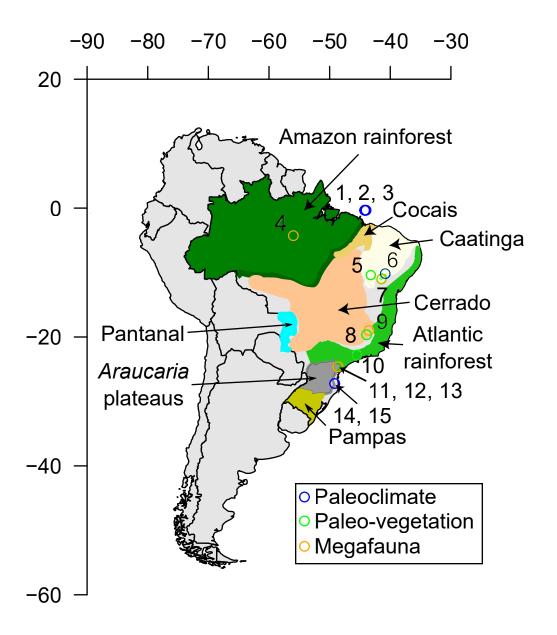


Fig 4. Map of Brazilian paleoclimate, paleo-vegetation, and Pleistocene megafaunal localities. This map is a Mercator projection, meaning that there is equal spacing between latitude lines and likewise for longitude. Axes show latitude and longitude in degrees. Color coding for bioregions in other parts of this manuscript is based on that in this map. Numbers represent paleoclimate, paleo-vegetation, and megafauna localities from Table 1 as follows: 1, 2, 3 = marine sediment cores BC 82, CDH 86, and GGC 81, respectively; 4 = Itaituba Quarry; 5 = Saquinho; 6 = Bahia; 7 = Gruta dos Brejoes; 8 = Lagoa Olhos D'Agua; 9 = Lapa dos Tatus); 10 = Morro de Itapeva (MDI); 11, 12, 13 = Abismo do Fossil Cave, Abismo do Iguatemi Cave, and Ribeira do Iguape, respectively; 14 = Botuverá Cave.

Table 2: Brazilian Paleo-vegetation, Paleoclimate, and Pleistocene Megafauna Localities. Color coding follows that of Figure 4.

15	14	13	12	<u> </u>
Botuvera Cave	Lagoa Dourada	Ribeira do Iguape	Abismo do Iguatemi Cave	Abismo do Fossil Cave
-27.2233, -49.1555	-25.2408, -50.0422	Ribeira do Iguape -24.6439, -48.6856	-24.58, -48.59	-24.58, -48.59
Paleoclimate	Paleoclimate	Megafauna	Megafauna	Megafauna
Speleothem	Lake sediments	Bone	Bone	Bone
Arancaria Plateaus	Arancaria Plateaus	Arancaria Plateaus	Arancaria Plateaus	Arancaria Plateaus
Cruz Jr. et al., 2005; 2006; 2007; Baker & Fritz, 2015	Moro et al., 2004	Neves, Hubbe, & Karmann, 2007; Hubbe et al., 2013	Hubbe et al., 2013	Hubbe et al., 2013

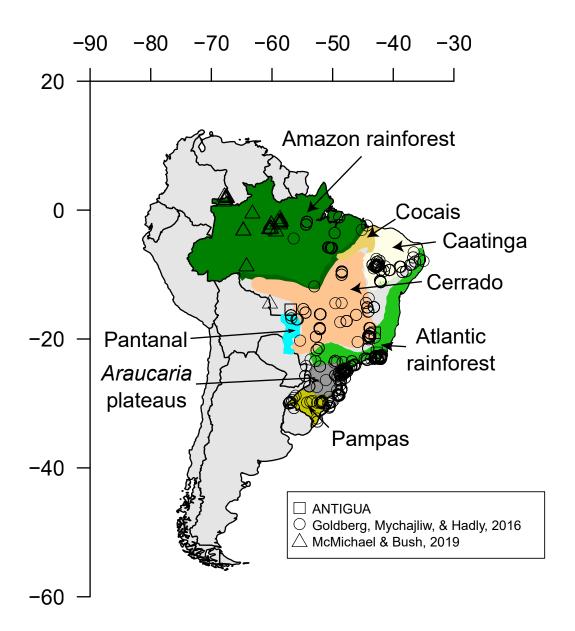


Fig. 5: Map of Brazilian archaeological localities. This map is a Mercator projection, meaning that there is equal spacing between latitude lines and likewise for longitude. Axes show latitude and longitude in degrees. Color coding for bioregions in this figure is based on that of Fig. 4. Squares represent ANTIGUA localities, circles represent Goldberg, Mychajilw, & Hadly (2016) localities, and triangles represent McMichael & Bush (2019) localities.

The Pampas

The Pampas is a region of low-relief, subtropical grasslands in south-southwestern Brazil and large parts of Argentina and Uruguay (Salgado, Santos, & Paisani, 2019). The grassland vegetation here is mostly herbaceous and shrubby plants (e.g., *Aristida jubata*; Family: Poaceae) thought to reflect a mixture of Cerrado and Argentinian steppe communities whose ranges have advanced and retreated in response to paleoclimatic changes (Verdum et al., 2019). Along with those herbs and shrubs, the Pampas also has riparian forests mostly made of palms (e.g., *Butia lallemantii*), leguminous trees (e.g., *Prosopis nigra*, *Vachellia caven*, and *Prosopis affinis*), and ironwood capons (e.g., *Myrachodruon balansae*; Family: Anacardiaceae) (Verdum et al., 2019). Average annual temperature and precipitation of the Pampas ranges from 17-23 °C and 1400-1800 mm, respectively (Verdum et al., 2019).

The Araucaria Plateaus

The Araucaria Plateaus line the southeastern Brazilian coast and have average annual temperatures of 12-18 °C (Gu et al., 2017). The higher-altitude areas of these plateaus, which have average winter temperatures of 15 °C and mean annual rainfall of 1700 mm (Ledru et al., 2005), host Brazil's Araucaria forests. These plateau forests are dominated by the conifers Podocarpus lambertii and Araucaria angustifolia (Salgado, Santos, & Paisani, 2019), and the angiosperms Mimosa scabrella, and Ilex (Gu et al., 2018). A. angustifolia—also known as the Brazilian pine (although not part of the Pinaceae Family)—is a long-lived conifer that reaches adult heights of 50 m and widths of 3 m (Salgado, Santos, & Paisani, 2019). It only tolerates well-drained sandy soils, so areas of the Araucaria Plateaus that have poorly-drained riparian forests are instead dominated by Sebastiania commersoniana—a leafy euphorb that can make up 80% of the individuals along these streams (Salgado, Santos, & Paisani, 2019).

At higher altitudes from these riparian forests, the montane communities in this bioregion are rich in *A. angustifolia* and *P. lambertii*, and these forests then transition to high montane steppes dominated by grasses (Salgado, Santos, & Paisani, 2019). In general, the vegetation of the Araucaria Plateaus is currently controlled by altitudinal gradients: differences in altitude translate to differences in groundwater and climatic regimes, which result in differences in plant communities. Also, there are many natural wetland reservoirs in this bioregion, which means that paleo-vegetation changes are well documented in palynological records from here (e.g., Ledru et al., 2005; Gu et al., 2017; 2018; Behling & Oliveira, 2018; and references therein).

The Atlantic Rainforest

The Atlantic Rainforest is just north of the *Araucaria* Plateaus in a 50-200 km wide strip (Gu et al., 2017) along the Atlantic coast of Brazil (Salgado, Santos, & Paisani, 2019), from the equator to 30° S (Ledru et al., 2005). Spanning this wide latitudinal range, the Atlantic rainforest also covers a broad spectrum of climates, from a more seasonal precipitation regime in the north, to a lack of dry season in the south (Ledru et al., 2005). Mean annual temperature ranges from 19-26 °C, mean summer highs range from 25-34 °C, and mean winter lows range from 14-18 °C (Kamino et al., 2019). Mean annual rainfall ranges from 1800-2400 mm along the coast to over 3600 mm further inland at higher elevations (Kamino et al., 2019). The Atlantic rainforest is also seasonally influenced

by both the ITCZ and ENSO: the former influences the length of the rainy season while the latter affects rainfall magnitude (Kamino et al., 2019). This forest is currently isolated from the Amazon rainforest by a drier strip of Caatinga, Cerrado, and Pampas, but was possibly connected to the Amazon in the past (see the 'Pleistocene arc hypothesis' below).

The plant community of this region is dominated by angiosperms from the families Orchidaceae, Fabaceae, Asteraceae, Bromeliaceae, Poaceae, Myrtaceae, Melastomataceae, Euphorbiaceae, Rubiaceae, and Apocynaceae, which mostly make up ombrophilous and seasonal vegetation (Kamino et al., 2019). Parts of these ombrophilous forests at elevations above 1,700 m have high abundances of *A. angustifolia* as well (Kamino et al., 2019). Some of this region's seasonal forests are defined by significant winter drought and intense summer rainfall, while others are defined by consistent annual rainfall and cold winters (mean monthly temperature < 15 °C) (Kamino et al., 2019). In these seasonal forests, 20-50% of the trees are deciduous (Kamino et al., 2019).

The Pantanal

The Pantanal is a relatively small (~150,000 km²), semi-arid bioregion of western Brazil that is well known for its extensive seasonal flooding during the austral summer (Boin et al., 2019). Mean annual rainfall of the Pantanal is only 1500 mm and is evenly distributed throughout the year, but the tributaries of the Paraguay River have marked upstream spikes in discharge rates between December and April. This leads to flooding from January to March (Boin et al., 2019). Being mostly inland, the Pantanal's temperature follows a relatively high amplitude pattern throughout the year, with temperatures ranging from average summer highs over 38 °C to average winter lows around 18 °C (Boin et al., 2019).

The vegetation here is a mix of plants from the Cerrado, Atlantic Rainforest, Amazon Rainforest, Caatinga, and the Gran Chaco (a savanna/open-forest biome of southwestern South America) (Boin et al., 2019). These plants include water hyacinths (*Euchhornia crassipes*), asthma plants (*Euphorbia hirta*), carpet and reimar grasses (*Reimarochloa*), caranday wax palms (*Copernicia alba*), and moriche palms (*Mauritia flexuosa*) (Boin et al., 2019). Many of the plants here tend to form floating mats and floating meadows as adaptations to the seasonal floods (Boin et al., 2019).

The Amazon Rainforest

The Amazon Rainforest is the largest bioregion of Brazil, being roughly the size of the contiguous US (Malhi et al., 2008). Situated about the equator with such a large area and density of vascular plants, transpiration in the Amazon accounts for 25-50% of its precipitation (Eltahir & Bras, 1994), making it very humid and warm year-round. The ITCZ and SASM are also responsible for bringing large quantities of oceanic water inland to the Amazon (Bueno et al., 2019). The Andes are responsible for stopping the trade winds from transporting this moisture any further west, which further increases the Amazon's annual rainfall (Bueno et al., 2019). These climatic conditions support a remarkable diversity of over 80,000 taxa of vascular plants (Colinvaux & De Oliveira, 2001), which can be grouped into *terra firme* forests, floodplain forests, and herbaceous areas subject to periodic flooding (Bueno et al., 2019).

Terra firme forests are the most dominant in the Amazon and form on dry soils (Bueno et al., 2019). These forests make up stratified, tall (up to 60 m) vertical habitats within the trees home to many epiphytes (Families: Orchidaceae and Areceae) and lianas (Families: Bignoniaceae,

Passifloraceae, Convolvulaceae, Hippocrateaceae, Apocynaceae, and Cucurbitaceae) (Bueno et al., 2019). Many plants in Amazonian floodplain forests have adaptations for seasonal flooding, including growth synchronized with the low-water season, loss of leaves from lower parts of the plants during floods, and fish- and water-dispersed seeds (Bueno et al., 2019). Similarly, mangroves are common around the mouth of the Amazon river in brackish waters (Bueno et al., 2019). The Amazon's herbaceous areas subject to periodic flooding are dominated by 1-9 m tall sclerophyll plants with pneumatophores that optimize gas exchange during flood events (Bueno et al., 2019).

The Cerrado

The Cerrado is a semi-humid savanna in central Brazil with dry austral winters and moist austral summers (MAP: 1200-1800 mm) (Salgado, Santos, & Paisani, 2019). Its mean annual temperature is 20-24 °C (Salgado, Santos, & Paisani, 2019) and its vegetation consists of ecotones from open forests and scrublands to open grasslands, with marshes alongside gallery forests (Salgado et al., 2019). The plants that make up this vegetation include Poaceae, *Acacia, Boscia, Byrsonima, Mimosa*-type, and *Didymopanax* distributed in grasslands and small patches of shrubs and small, gnarly trees (*cerradão* = open forest) (Salgado-Labouriau et al., 1998). The Cerrado's marshes are important areas for wetland sediment records (e.g., Cassino, Martinho, & Caminha, 2018). Also, this bioregion currently supports many charismatic Brazilian savanna fauna—including the jaguar (*Panthera onca*), giant anteater (*Myrmecophaga tridactyla*), puma (*Puma concolor*), tapir (*Tapirus terrestris*), capybara (*Hydrochoerus hydrochaeris*), and the maned wolf (*Chrysocyon brachyurus*) (Salgado et al., 2019)—and was likely suitable habitat for many Brazilian Pleistocene megafauna.

The Caatinga

The Caatinga is a semi-arid grassland/shrubland/thorn-shrub-savanna that covers 850,000 km² in northeastern Brazil (Behling et al., 2000). Its name is derived from the indigenous Tupi-Guarani word for white forest, which refers to the landscape's dry, washed-out appearance after the deciduous plants here shed their leaves (de Barros Corrêa et al., 2019). The Caatinga has a 6-11 month hot, dry season, with average annual precipitation often less than 250-750 mm (Behling et al., 2000). The annual amplitude of temperature change is relatively minor though, with summer and winter averages ranging from 26-28 °C and 20-26 °C, respectively (de Barros Corrêa et al., 2019). The contradictory nature of low precipitation in this equatorial bioregion comes from the South Atlantic High (an atmospheric high pressure cell) that regularly displaces the ITCZ to the north (de Barros Corrêa et al., 2019).

The vegetation adapted to this climate includes mostly Poaceae, *Borreria*, and Mimosaceae; however, patches of deciduous forest, gallery forest, and floodplain vegetation exist here too (Behling et al., 2000). These plants can be woody, herbaceous, or succulents (e.g., Family: Cactaceae), and are largely (~80%) restricted to lowlands (de Barros Corrêa et al., 2019). The presence of minor gallery forests in the Caatinga and its position between the Amazon and Atlantic rainforests have suggested to some that the Caatinga may have acted as a corridor between these two rainforests under past climatic regimes (Bouimetarhan et al., 2018) (see 'Pleistocene arc hypothesis' below).

The Cocais

The Cocais is an ecotonal landscape dominated by *Cocais* palm trees (Family: Arecaceae) between the Amazon rainforest, the Cerrado, and the Caatinga (Salgado, Santos, & Paisani, 2019). Being at the intersection of these bioregions, the Cocais has a mixed pattern of humid equatorial, semi-arid tropical, and semi-humid tropical climates (Salgado, Santos, & Paisani, 2019). Rainfall patterns in this bioregion are abnormal—instead of a spectrum between wet and dry seasons or persistent annual dry or wet conditions, the Cocais' wet season migrates from the south, to the east-central part of the bioregion, and then to the north over the span of October to July (Salgado, Santos, & Paisani, 2019). Mean annual temperatures in the eastern, semi-arid tropical Cocais range from 20-28 °C, whereas those in the humid equatorial Cocais closer to the Amazon in the west range from 26-28 °C (Salgado, Santos, & Paisani, 2019). Some workers have noted that the presence of palms interspersed by herbaceous fields in this region may be indicative of disturbance through deforestation or burns (Salgado, Santos, & Paisani, 2019). On that note, historical anthropogenic disturbance here largely occurred between the 1700s and 1800s, meaning that the current presence of palm savannas in this landscape might be a successional legacy of recent disturbance at the Amazon's edge (Salgado, Santos, & Paisani, 2019).

Quaternary paleovegetation of Brazil

In the absence of studies of non-Recent Brazilian Quaternary macroflora, genetic and palynological data have provided all of the insights regarding Brazil's Quaternary paleovegetation. Genetic studies have focused on the Amazon Rainforest's extremely high genetic diversity, especially regarding the 'Amazonian refugia hypothesis' of Haffer (1969). This hypothesis posits that during Pleistocene glacial maxima, the Amazon was isolated into patches of forest surrounded by savannas and grasslands, resulting in allopatric speciation and the resultant genetic diversity observable today (Arruda et al., 2018). A "pollen gap" for the LGM of this region precludes testing this hypothesis with palynological data (Baker & Fritz, 2015), leaving the phylogeography of the Amazon tantalizing and controversial (e.g., Da Silva & Patton, 1998; Leite et al., 2016). A similar biogeographic idea surrounding Brazil's vegetation is the 'Pleistocene arc hypothesis' of Prado and Gibbs (1993), which hypothesizes that the Amazon and Atlantic rainforests were connected in the Pleistocene through the Caatinga but have since separated, with the resultant allopatry explaining the genetic diversity and differences between the two biomes (Arruda et al., 2018).

Although existing palynological records have not resolved the history of the Amazon to the extent needed to fully understand current diversity there, the records are extremely valuable in reconstructing Quaternary vegetation in some parts of Brazil. These studies include lake sediment records from the Amazon rainforest (e.g., Hermanowski et al., 2012; Castro et al., 2013; Fontes et al., 2017; Arruda et al., 2018; and D'Apolito, Latrubesse, & Absy, 2018), two marine cores off of the northeastern coast of Brazil (Behling et al., 2000; Bouimetarhan et al., 2018), two palm swamp records from the Cerrado (Salgado-Labouriau et al., 1998; Cassino, Martinho, & Caminha, 2018), and many palynological records from the Atlantic rainforest in southern and southeastern Brazil (for a comprehensive overview, see Behling, 2002).

Archaeology of Brazil

The archaeological record of South America suggests that paleo-humans likely arrived through Central America in a singular event and then followed the Atlantic coast to Brazil ~13,000-12,000 Cal (meaning calibrated/calendar) yr BP (Goldberg, Mychajliw, & Hadly, 2016). Interestingly, many of the oldest South American archaeological sites are from the far southern reaches of Patagonia (e.g., Dillehay et al., 2015), although radiocarbon data substantiate the hypothesis that the first South Americans made their way through Central America (Goldberg, Mychajliw, & Hadly, 2016). This suggests that the first South Americans quickly passed through Brazil before establishing more persistent sites further south.

While human populations in other South American regions were expanding from the late Pleistocene through the Holocene, paleo-demographic inferences of Brazil's population suggest that it was quite stable throughout the Holocene until 2,000 Cal yr BP (Goldberg, Mychajliw, & Hadly, 2016). Goldberg, Mychajliw, & Hadly (2016) also estimated that Brazil was sparsely populated from 14,000-2,000 Cal yr BP relative to other South American regions. There have also been at least two verified Pleistocene megafaunal kill sites in Brazil—one of a disjointed and butchered *Eremotherium* at Toca da Boa Vista cave in southern Brazil and another of a *Notiomastodon platensis* ilium from Lagoa Santa in Minas Gerais, with possible butcher marks (Prous & Fogaca, 1999). However, neither of these specimens have been numerically dated, so they are not included in this study.

Methods

Paleoclimate and paleo-vegetation

Paleoclimate and paleo-vegetation records were extracted from a Web of Science search (https://clarivate.com/webofsciencegroup/solutions/web-of-science/) that focused on locating records that spanned the Pleistocene-Holocene transition and were geographically closest to megafaunal localities (Fig. 4). When possible, all radiocarbon records were re-calibrated using CALIB v. 7.1.0 (http://calib.org/calib/). For all outputs of calibrated dates, I selected only the 2σ age ranges that corresponded to the highest relative areas under each curve. For example, this means that for a given date with two possible age distributions under the calibration curve, I selected the distribution that accounted for the greatest area under the curve and did not report the other. Also, all dates were calibrated using the SHCal13 southern hemisphere calibration curve (Hogg et al., 2013) unless otherwise noted. The exceptions include marine sediment core records from Nace et al. (2014), which were calibrated using the Fairbanks0107 calibration curve (Fairbanks et al., 2005) and archaeological dates from north of the equator that were calibrated using IntCal13 (see **Humans** below). The uncalibrated values from Nace et al. (2014) were unavailable for comparison.

The Fairbanks curve is derived from radiocarbon and ²³⁰Th/²³⁴U/²³⁸U dates sampled from offshore coral reefs for 50,000-0 Cal yr BP. In contrast, the SHCal13 curve is derived from southern hemisphere tree ring data for the Holocene, and the main difference between Fairbanks0107 and SHCal13 is that the former is based on a Bayesian statistical model while the latter is based on a random walk statistical model. This difference does not account for any notable variation between calibration datasets for the timeframe of the study here. For dates 50-12 ka, the SHCal13 curve is the

same as the northern hemisphere IntCal13 curve but with an average offset of 43 ∓ 13 yr (Hogg et al., 2013). This offset is to correct for southern hemisphere dates being systematically older due to an oceanic old-carbon reservoir effect (Hogg et al., 2013). The 50-12 ka dates on the IntCal13 curve in turn are derived from terrestrial plant macrofossils in varved lake sediments, U-series dated speleothems, and U-Th dates from marine records (Reimer et al., 2013).

We used the following paleo-climate proxies. For the marine sediment cores Nace et al. (2014), seawater ice-volume corrected $\delta^{18}{\rm O}$ values ($\delta^{18}{\rm O}_{\rm swive}$) provided the paleo-effective-moisture proxy. Given that global variations in both sea water temperature and ice volume can affect marine $\delta^{18}{\rm O}$ values (Delaygue, 2009), Nace et al. (2014) reported $\delta^{18}{\rm O}_{\rm swive}$ as a signal primarily of salinity. The locality where these sediments were cored is close to the Amazon River delta, such that Nace et al. (2014) attributed more negative $\delta^{18}{\rm O}_{\rm swive}$ values in this record to freshwater isotopic dilutions during pluvial events. Therefore, these values can be used as a proxy for paleo-effective-moisture in this region.

For cave records, paleo-effective-moisture proxies came from speleothem and travertine growth-period records in northeastern Brazil (the Caatinga) (Wang et al. 2004), and from δ^{18} O_{VPDB} values from a speleothem in Botuverá Cave in southern Brazil (The *Araucaria* Plateaus) (Figures 4 & 5). For the speleothem and travertine growth period records, Wang et al. (2004) argued that growth of these formations only occurs during events where groundwater infiltration is sufficient to deposit calcite. Therefore, periods of speleothem and travertine growth are thought to represent pluvial periods as well. Lastly for paleo-effective-moisture records, the δ^{18} O record from Botuverá Cave (speleothem Bt2) is thought to primarily reflect local precipitation and upstream rainfall/transpiration (Cheng et al., 2013). These values, however, do not account for temperature effects and amount effects during the LGM. Baker & Fritz (2015) later corrected the values for those effects, so I used their measurements instead (Fig. 6).

For a paleo-temperature proxy, I used Mg/Ca-derived sea-surface temperatures (SSTs) from the Nace et al. (2014) marine sediment cores (Figures 4 & 6). The paleo-SST record of Fig. 5 is derived from Mg/Ca ratio measurements (see Higginson, 2009) on the planktonic foraminifer *Globigerinoides ruber*, extracted from the cores taken by Nace et al. (2014).

The pollen records from the paleo-vegetation reflected the regional taxa in each area, thus the taxa involved differed from site to site (e.g., *Araucaria* pollen from southern Brazil, Caatinga plant pollen from northeastern Brazil). I summarized changes in paleo-vegetation inferred from each pollen record by grouping general pollen types together (e.g., pollen types from herbaceous plants vs. those from *Araucaria* forest trees) per each locality so that they could be compared between sites more easily. The age model for each paleo-vegetation site was based on a linear interpolation between radiocarbon dates. Figures 6 and 7 compare the vegetation changes so determined, the paleo-temperature and paleo-humidity proxies, and the timing of extinction derived by the GRIWM analyses.

The analyses for selecting megafaunal/archaeological radiocarbon dates and estimating extirpation/arrival dates (Figs. 4-7) in this study were done using R (R Core Team, 2020).

Megafauna

To curate a chronology of megafaunal extirpation with locality information for Brazil, I started with 355 radiocarbon dates for South American megafauna in the ANTIGUA dataset and winnowed that down to the 25 dates reported for Brazilian megafauna specifically. I then winnowed that further down to the 13 radiocarbon dates considered robust by the rating scale reported by Barnosky and Lindsey (2010) (Table 3) All of these dates were obtained from the ANTIGUA project—a collaborative effort of more than 40 North- and South-American workers—and ranked > 10 sensu Lindsey & Barnosky, 2010. I confirmed with Dr. Alexander Hubbe—the ANTIGUA project expert in Brazilian archaeology and paleontology—to verify that these dates encompass all known, high-quality Brazilian Pleistocene megafauna radiocarbon dates as of October 2019. I avoided dates on bioapatite because bioapatite from both bone and enamel undergoes substantial isotopic exchange with the surrounding sediment during fossilization, which alters the isotopic ratios of interest (Zazzo & Saliège, 2011). I note that there might be more megafauna dates in the Brazilian non-English literature, but if so, I am unaware of them.

Table 3: Radiocarbon dates, Calibrated dates, and estimated extirpation date for Brazilian late-Pleistocene megafauna. Color coding follows that of Figure 4.

Abismo do Fossil Cave Araucaria Plateaus 12 Abismo do Iguatemi Cave				o	Caatinga 7	Rainforest	Amazon	Site number Bioregion from Fig. 4			
Abismo do		Fossil Cave	Abismo do			Lapa dos Tatus	Gruta dos Brejoes	randoa Zuarry	Itaituba Oua rr v	Site name	
Catonyx cuvieri	Toxodon platensis	Eremotherium laurillardi	Scelidotherium sp.	Glyptodon clavipes	Caronyx invien	Catoanis Marion	Nothrotherium maquinense	Eremotherium laurillardi	Notiomastodon platensis	Species	
Beta 230974	Beta 237347	Beta 237348	Beta 237349	Beta 237350	Beta 174689	Beta 174688	NZA 6984	Beta "sample 2"	Beta NA	Lab code	
10800, 60	11850, 70	12550, 60	15780, 80	17800, 70	13920, 50	14030, 50	12200, 120	11340, 50	15290, 70	¹⁴ C age, ∓ sd (yr BP)	
12753 - 12637	13761 - 13474	15084 - 14304	19204 - 18797	21786 - 21229	17037 - 16552	17209 - 16708	14637 - 13748	13267 - 13065	18698 - 18330	age range (Cal yr BP)	2σ calibrated
Hubbe et al., 2013	Hubbe et al., 2013	Hubbe et al., 2013	Hubbe et al., 2013	Hubbe et al., 2011	Lindsey, 2010	Barnosky &	Auler et al., 2006	et al., 2013	Rossetti et al.,	References	

13		
Ribeira do Iguape		
Toxodon platensis		Smilodon populator
Beta 218193	Beta 215330	Beta 183566
11090, 40	11380, 40	14580, 90
13051 - 12780	13280 - 13088	17956 - 17471
& Karmann, 2007; Hubbe et al., 2013	Neves, Hubbe,	Hubbe et al., 2013

Because last-appearance dates (LADs) usually precede actual extinction dates (the Signor-Lipps effect; Signor III & Lipps, 1982) and vice versa for first-appearance dates (FADs), I applied the Gaussian-resampled, inversely weighted McInerny et al. (GRIWM) method (Bradshaw et al., 2012) to obtain estimates of megafaunal extirpation and human arrival. I chose GRIWM over alternatives because it is highly accurate, accounts for date uncertainties, and is not prone to Type I or II errors (Bradshaw et al., 2012) The GRIWM method works as follows: The initial, calibrated dates are first resampled in a Gaussian manner, such that the extremes of the date distribution are less likely to be resampled than the central values. Then, the temporal distance of each resampled occurrence is inversely-weighted relative to the most recent occurrence for estimating extirpation, and to estimate arrival, relative to the least recent occurrence. The shorter the time interval between a given date and the most recent one (a rough indicator suggesting relatively high population size), the further from the LAD the actual extinction date is estimated to be. The converse holds true for estimating how much earlier an actual arrival date is than the FAD.

To run the GRIWM method on my dates, I modified a script from Saltre et al. (2015) to perform the GRIWM method and created a "GRIWM" R package for reproducibility (https://github.com/sarakahanamoku/GRIWM). Because the majority of the megafauna dates come from southern Brazil (n = 8 out of 13, see Fig. 4 for locality locations), I applied the GRIWM method to this vetted radiocarbon subset and then compared the subset to a subset consisting of LADs for all other vetted Pleistocene megafauna radiocarbon dates to assess whether timing of exptirpation in southern Brazil differed from that elsewhere (Figs 6 & 7). No significant differences were found, so the following discussion is based on the complete set of 13 dates.

Humans

I filtered Brazilian archaeological dates from the ANTIGUA dataset for quality (n = 33 of 70) as I did for the megafauna dates (see *Megafauna*) above. To get a larger sample size of archaeological dates from Brazil, I also included dates from Goldberg, Mychajliw, & Hadly (2016) and McMichael & Bush (2019).

Because the Goldberg, Mychajliw, & Hadly (2016) dataset is for all of South America, I selected only those archaeological dates within Brazil. This dataset includes dates from English, Spanish, French, and Portuguese publications, and excludes dates that have been questioned in the literature. Thus, this dataset has yet to be vetted for quality *sensu* Barnosky & Lindsey (2010), but is very comprehensive. The McMichael & Bush (2019) dataset focuses on archaeological dates from the region of Amazonia, which includes some from outside of the Brazilian Amazon rainforest (e.g., those from the Peruvian Amazon Rainforest). To select only Brazilian dates from this dataset, I read a shapefile of Brazil into R and selected only those values that fell within the bounds of this shapefile. Like the Goldberg, Mychajliw, & Hadly (2016) dataset, these dates were not vetted for quality using the Barnosky and Lindsey (2010) criteria.

After obtaining a bulk archaeological dataset with 1,377 dates, I removed those that were redundant between datasets, which reduced the sample size to 1,163 dates. Of those, 1,031 of those dates are from the Goldberg, Mychajliw, & Hadly (2016) dataset and 129 dates are from the McMichael & Bush (2019) dataset. The analyzed data set included the 33 vetted dates from ANTIGUA, 30 of which also were reported in the Goldberg, Mychajilw, & Hadly (2016) and McMichael & Bush (2019 (see Appendix 1 for all 1,377 archaeological dates). I performed two GRIWM arrival estimates—one for the combined Goldberg, Mychajilw, & Hadly (2016) dataset to

estimate human arrival within Brazil as a whole, and one just on the McMichael & Bush (2019) dataset to estimate human arrival time in the Brazilian Amazon Rainforest (Table 3, Figures 3 & 4).

Table 4: Estimates for first human arrival and megafaunal extirpation in Brazil.

Arrival or extirpation	Original dataset reference	Focal region	Number of dates	Age range of GRIWM estimate (Cal yr BP)	Centroid of GRIWM estimate (Cal yr BP)
Arrival	Goldberg, Mychajliw, & Hadly, 2016	All of Brazil	1,031	22,893 - 16,005	17,950
Arrival	McMichael & Bush, 2019	Amazon Rainforest	129	8,894 - 6,642	7,781
Extirpation	ANTIGUA	All of Brazil	13	12,656 - 11,696	12,110

Results

Lumping megafaunal extirpation dates from all regions for the GRIWM analysis estimated an extirpation date of 12,656-11,696 Cal yr BP (Table 4). During this extirpation period, the paleo-effective-moisture and paleotemperature proxies of northern Brazil show no directional trends, but the loss of megafauna does correspond with an increase in effective moisture and slight decrease in temperature in northern Brazil and with a decrease in effective precipitation on the southern Brazil *Araucaria* Plateaus (Fig. 6). At the same time in the Cerrado, herb pollen increases at the expense of tree pollen (Fig. 7), indicating opening of the landscape that would be consistent with a decrease in effective moisture. In the Atlantic Rainforest, *Araucaria* forest pollen essentially disappears coincident with the lower boundary of the extinction window. Taken in concert, this pattern suggests a series of paleoenvironmental changes corresponded with the timing of extinction.

For the LADs of the megafauna taxa taken individually, no paleoclimate or paleo-vegetation events correspond with apparent losses of individual taxa, except for a decrease in *Araucaria* forest and a dry spell coinciding with the toxodon LADs (~14,000-13,000 Cal yr BP). However, the *Glyptodon*, *Notiomastodon*, *Smilodon*, and three of the seven ground sloth LADs overlap with the human arrival estimate. As for any potential trends in the relative chronology of megafauna LADs, larger herbivores seem to have earlier LADs than smaller herbivores.

For archaeological dates, the Goldberg, Mychajilw, & Hadly (2016) dataset for all of Brazil (n = 1,031 dates) yielded a human arrival estimate of 22,893-16,005 Cal yr BP, with a centroid value of 17,950 Cal yr BP (Figs 6 & 7, Table 4). The McMichael & Bush (2019) dataset focusing on the Brazilian Amazon Rainforest (n = 129) yielded a human arrival estimate of 8,894-6,642 Cal yr BP, with a centroid value of 7,781 yr BP (Table 4), which is substantially younger than the estimate for all of Brazil. This is also substantially younger than other evidence for human occupation in the Amazon ~13,000 Cal yr BP (Roosevelt, 2013).

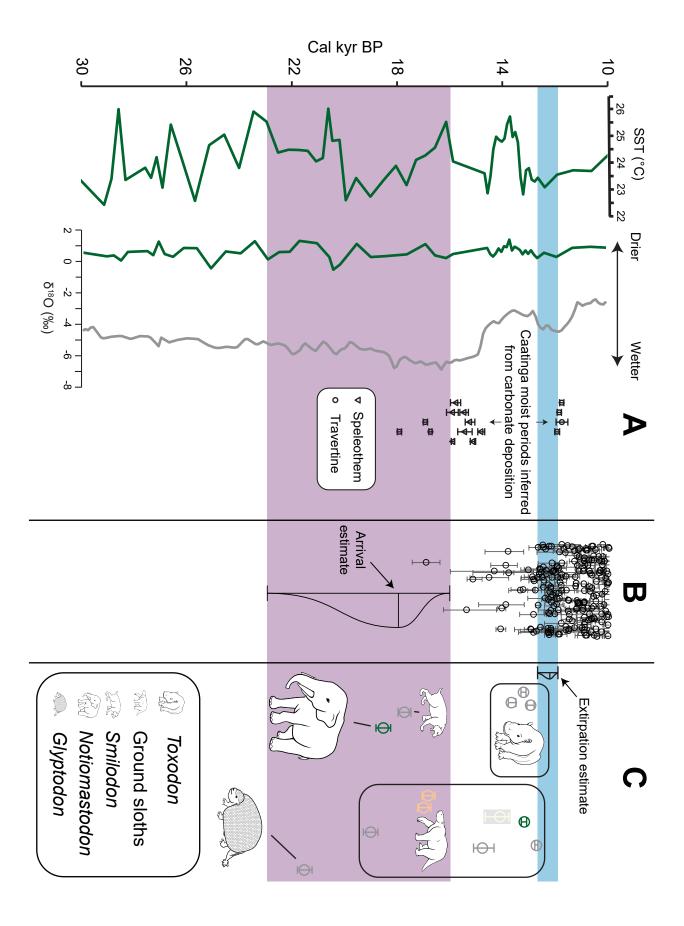


Fig 6. Brazilian paleoclimatic changes surrounding Pleistocene human arrival and megafaunal Extirpation.

- A. Paleoclimate records of Brazil. Color coding corresponds to the bioregion coloring of Fig. 3. Left curve—the composite Mg/Ca-derived sea surface temperature (SST) records from cores BC 82, CDH 86, and GGC 81 collected near the northeast Brazilian coast. Middle curve—the composite δ¹⁸O_{swive} records from cores BC 82, CDH 86, and GGC 81 collected near the northeast Brazilian coast. Right curve—the Baker & Fritz (2015) corrected δ¹⁸O_{VPDB} record from Botuverá Cave speleothem Bt2 in southern Brazil. Points with error bars—growth periods from speleothems (triangles) and travertines (circles) at the Bahia locality (Caatinga bioregion).
- B. Archaeological dates for Brazil from Goldberg, Mychajilw, & Hadly (2016). Confidence intervals about circles represent 2σ calibrated age ranges; circles represent the median values per each age. Purple area shows the GRIWM-estimated Brazil arrival date of 22,893-16,005 Cal yr BP, with a centroid value of 17,950 Cal yr BP (see Table 4). Only the dates younger than 10,000 Cal yr BP are shown here—193 of the 1,031 total from Goldberg, Mychajilw, & Hadly (2016). All 1,031 of these went into the GRIWM estimate however. Because none of the McMichael & Bush (2019) dates are older than 10,000 Cal yr BP, they are not shown here.
- C. High-quality calibrated Pleistocene megafaunal radiocarbon dates and GRIWM-estimated extirpation date. Illustrations denote which dates correspond to which megafauna taxa. Confidence intervals about circles represent 2σ calibrated age ranges, circles represent the median values per each age, and their colors correspond to the bioregion color coding from Fig. 1. Blue area shows the GRIWM-estimated extirpation date of 12,656-11,696 Cal yr BP with a centroid value of 12,110 Cal yr BP (see Table 4).

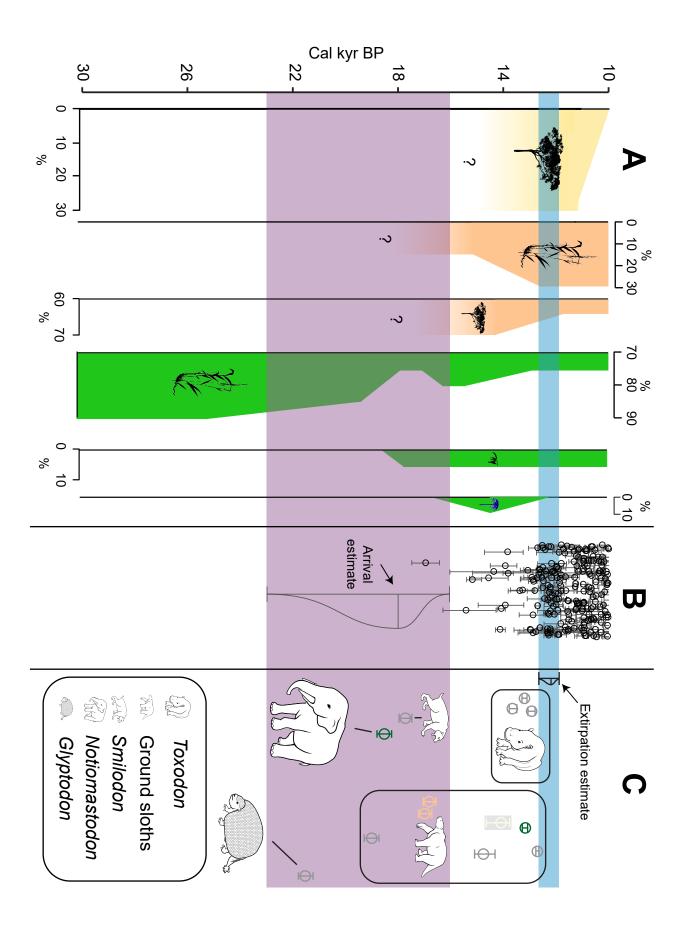


Fig. 7: Brazilian paleo-vegetational changes surrounding Pleistocene human arrival and megafaunal Extirpation.

- A. Paleo-vegetation records of Brazil. Color coding corresponds to the bioregion coloring of Fig. 3. **Curves, from left to right:** Caatinga tree pollen indicators from Saquinho; herb and tree pollen indicators from the Lagoa Olhos D'Agua locality in the Atlantic Rainforest of southeastern Brazil.; and grassland, Atlantic rainforest, and *Araucaria* forest (includes trees and other plants) pollen indicators from the Morro de Itapeva locality in the Atlantic Rainforest of southern Brazil. Caatinga and Cerrado pollen indicators from SAN make up < 1% of the pollen sum, hence, were not included in this figure. Question marks and color gradients reflect that pollen relative abundances for times older than these points are unknown. See Table 2 for further locality information.
- B. Same as in Fig. 6: Archaeological dates for Brazil from Goldberg, Mychajilw, & Hadly (2016). Confidence intervals about circles represent 2σ calibrated age ranges; circles represent the median values per each age. Purple area shows the GRIWM-estimated Brazil arrival date of 22,893-16,005 Cal yr BP, with a centroid value of 17,950 Cal yr BP (see Table 4). Only the dates younger than 10,000 Cal yr BP are shown here—193 of the 1,031 total from Goldberg, Mychajilw, & Hadly (2016). All 1,031 of these went into the GRIWM estimate though. Because none of the McMichael & Bush (2019) dates are older than 10,000 Cal yr BP, they are not shown here.
- C. Same as in Fig. 6: High-quality calibrated Pleistocene megafaunal radiocarbon dates and GRIWM-estimated extirpation date. Illustrations denote which dates correspond to which megafauna taxa. Confidence intervals about circles represent 2σ calibrated age ranges, circles represent the median values per each age, and their colors correspond to the bioregion color coding from Fig. 3. Blue area shows the GRIWM-estimated extirpation date of 12,656-11,696 Cal yr BP with a centroid value of 12,110 Cal yr BP (see Table 4).

Discussion

Hypothesis 1: Defaunation

Regarding hypothesis 1—that megafauna extirpation caused vegetation changes—no notable vegetation change is evident directly after the estimated extirpation, except for an early-Holocene decline in Caatinga tree pollen. This postdates the minimum age of the extirpation by ~200 yr (Fig. 7). These observations lead to rejection of hypothesis 1 in a general sense. However, the Caatinga tree pollen decline that postdates the extirpation window by ~200 yr (Fig. 7) may represent a more localized defaunation signal. This is difficult to definitively claim though with only one high-quality Caatinga megafauna date (a ground sloth dated 14,637-13,748 Cal yr BP, see Table 3). If this Caatinga defaunation signal is true, however, Mimosaceae trees would have been likely most affected, given they make up most of the Caatinga's tree vegetation (see **The Caatinga** above). Interestingly, some of these Caatinga trees can survive and resprout after extreme coppicing, pollarding, and crown thinning (Figueirôa et al., 2006), suggesting that they might be adapted to Pleistocene megafaunal browsing. Though there are not any known studies that have investigated megafaunal endozoochory of Caatinga tree seeds, a lack of seed dispersal following Caatinga

megafaunal extirpation led to the observed decrease in tree pollen. However, these trees are widely used today for wood and charcoal (Figueirôa et al., 2006), so perhaps their inferred decline was due to an increase in these human behaviors at this time to some degree—the decline in Caatinga tree pollen also coincides with the aforementioned increase in archaeological dates. Altogether, Hypothesis 1 can be rejected outside of the Caatinga, but it cannot currently be resolved whether defaunation and/or anthropogenic activities might have caused the inferred Caatinga tree decline.

Hypothesis 2: Habitat loss led to megafaunal decline

The Caatinga and Atlantic Rainforest pollen records do not support Hypothesis 2, but the Cerrado and *Araucaria* Plateau records may.

In the Cerrado, the pollen record suggests a shift from forested to herbaceous landscapes. The culmination of this trade-off in pollen groups coincides with the estimated extirpation dates, particularly of toxodonts, but for all megafauna taken as a whole. *Toxodon* was a mixed C₃ feeder and C₄ grazer (Lopes et al., 2013; Pansani et al., 2019), meaning that *Toxodon* may have been more able to switch feeding habits with habitat change. If habitat loss correlates with *Toxodon* decline then, this might mask some other cause for the decline, e.g., increased competition with other species. An increase in herbaceous pollen and decrease in tree pollen suggests an opening of the landscape and less large woody vegetation, which could have been an important dietary component for some of the extinct megafauna (da Silva et al., 2019; Pansani et al., 2019; Asevedo et al., 2020). Interestingly, this vegetation shift coincided with increasing effective moisture, which would be expected to favor forest expansion over grassland, not the other way around. The estimated human arrival time precedes both of these vegetation changes, so perhaps anthropogenic landscape clearing led to these vegetation changes, an indirect pressure that eventually led to habitat loss and megafaunal decline.

The changes in Araucaria Plateau forest pollen from the Atlantic Rainforest of southern Brazil are interesting as well. Ledru, Mourguiart, & Riccomini (2009) noted that high abundances of Araucaria forest pollen tend to correlate with high effective moistures throughout the Pleistocene, and Cárdenas et al. (2019) found that initial southern Brazil Araucaria forest expansion in the mid-Holocene at 4,000 Cal yr BP also correlates with increased effective moisture. However, Cárdenas et al. (2019) also noted that later Holocene Araucaria forest expansion no longer correlated with wetter conditions. Therefore, the presence of Araucaria forests inferred from pollen records is not dependent upon climate alone. Robinson et al. (2018) used a neutral landscape model approach to suggest that recent Araucaria forest expansions from 1,410-900 Cal yr BP were due do cultivation of Araucaria trees for their large and nutritious Araucaria "pine nuts"—a legacy that can be seen in the distribution of A. angustifolia today. The earliest dates for Araucaria cultivation are unknown, but the relatively large seed size of Araucaria has led many authors to suggest that some form of cultivation is necessary for seed dispersal (Robinson et al., 2018). Parrots (Tella et al., 2019) and parakeets (Shepherd et al., 2008) are known to be effective Araucaria dispersal agents while rodents are known to be Araucaria seed predators (Viera et al., 2011), so a combination of human cultivation, parrots and parakeets dropping seeds, rodents forgetting or abandoning Araucaria seeds, and/or megafaunal endozoochory could be involved in Araucaria seed dispersal.

Linking back to *Araucaria* forest habitat loss, an increase in *Araucaria* forest pollen coincides with the younger bound for the human arrival window, and the inferred Pleistocene-Holocene disappearance of *Araucaria* forests lines up with the older bound for the megafaunal extirpation window. This might initially suggest that the loss of *Araucaria* forests can be implicated in the

megafaunal extirpation, but prior to ~16 kyr BP, *Araucaria* forest pollen levels at MDI (Locality 10, Fig. 4, Table 1) were 0% (Fig. 7). Perhaps a combined effect of human landscape modification superimposed on *Araucaria* forest decline was involved in the extirpation, but this cannot currently be verified.

Hypothesis 3: Climate-driven extirpation

Regarding Hypothesis 3—that climate change caused the extirpation—temperature and effective moisture in northern Brazil do not notably change preceding the extirpation period, but effective moisture does change in the Caatinga and *Araucaria* Plateaus at this time (Fig. 6). In the Caatinga, tree pollen quantity does not coincide with this, but at the *Araucaria* Plateaus, the decline in *Araucaria* forest pollen does match a dry period that interrupted a \sim 15+ kyr trend in increasing effective moisture (Figs 6 & 7). The extirpation window started right as this dry period ended, as inferred from *Araucaria* Plateau δ^{18} O values and resumed Caatinga carbonate growth (Fig. 6). Therefore, it is not possible to firmly reject the climate change hypothesis on the basis of these data.

Hypothesis 4: Anthropogenic extirpation

Lastly, regarding Hypothesis 4—that human pressures caused megafauna loss—it is clear that human arrival preceded megafaunal extirpation (Figs 6 & 7), and also coincided with LADs of glyptodonts, proboscideans, sloths, and *Smilodon*. If that human pressure took the form of habitat modification, competition for resources, and/or direct hunting, it may well have reduced population sizes enough to cause local population crashes. As noted in the **Results**, the LADs of larger bodied taxa are earlier than those of smaller bodied taxa, which would be consistent with animals with the smallest population sizes and longest generation times (an inverse correlate of body size) being affected earlier than smaller-bodied animals as human populations moved into the area and began to infringe on the animal populations. However, megafauna clearly persisted for at least five thousand years after humans arrived in the various areas. Therefore, while it is impossible to reject the hypothesis that humans contributed to gradual attrition of megafauna populations, it is clear that they did not cause sudden extinctions here.

Pleistocene extirpations in other regions of South America

My estimated bulk extirpation date of 12,656-11,696 Cal yr BP for Brazil is coeval with the 12,000-11,100 Cal yr BP estimate for southern Brazil based on *Sporormiella* from Raczka, Bush, & De Oliveira (2018), and overlaps that for ground sloths, equids, *Macrauchenia*, and *Toxodon* in the nearby Pampas of Argentina, all ~13,000 to 9,000 Cal yr BP (Barnosky & Lindsey, 2010). The difference on the younger end of these age ranges might be due to dietary constraints of taxa and habitat differences between these regions (see **Dietary considerations** below).

The next closest region with comparable data is southwestern Patagonia (Villavicencio et al., 2016). My estimated extirpation window of 12,656-11,696 Cal yr BP resembles that for that of Pleistocene-Holocene Patagonian felids, equids, and *Lama* cf. *owenii*, but does not overlap the extirpation estimate of ~11,000-8,000 Cal yr BP for ground sloths in Patagonia.

My 22,893-16,005 Cal yr BP estimate of human arrival in Brazil falls at least ~1,500 yr earlier than the Patagonian estimate of Villavicencio et al. (2016), but overlaps the Monte Verde ~18,500-14,500 Cal yr BP age estimate as the oldest archaeological site in Chile (Dillehay et al., 2015). Gomez-Carballa et al. (2018) used genomic data to investigate outhward dispersal from Central to South America along both the Pacific and Atlantic coasts. Therefore, my arrival estimate may suggest that there were human populations dispersing southward along the Atlantic coast as quickly as those along the Pacific coast, as prehistoric trans-Andean human dispersal is thought to be unlikely (Gómez-Carballa et al., 2018).

This is later than the estimated extirpation time of 15,800 Cal yr BP in Peru (Rozas-Dávila-et al., Valencia, & Bush, 2016), but Rozas-Dávila, Valencia, & Bush-et al. (2016) argue that the Peruvian extirpation was not due to human activity—15,800 Cal yr BP is much earlier than any verified archaeological dates in this region. Rather, the Peruvian extirpation is thought to coincide with warm, wet intervals that resulted in the loss of important floras and subsequent megafaunal extirpation, i.e., an example of the mosaic-nutrient hypothesis of Guthrie (1984).

Dietary considerations

 C_3 plants photosynthesize sugars from water and CO_2 using phosphoglycerate—a three carbon molecule—as an intermediary, but C_4 plants are more photosynthetically efficient and dominant in Brazilian grasslands (Edwards et al., 2010). These two plant community types and their metabolic pathways can be picked up by their differences in photosynthate molecular weights, leaving distinctive $\delta^{13}C$ signatures in animal tissues, such as enamel (Koch, 2007). $\delta^{13}C$ values from South American megafauna enamel suggest that these taxa varied in their C_3/C_4 intake.

South American ground sloths tended to be C_3 browsers (Pansani et al., 2019), *Toxodon* was a mixed C_3 feeder and C_4 grazer (Lopes et al., 2013; Pansani et al., 2019), South American equids were almost exclusively C_4 grazers (Pansani et al., 2019), and *Macrauchenia* was a mixed C_3/C_4 feeder (MacFadden & Shockey, 1997). Although this may give the impression that these dietary habits are diagnostically associated with these taxa (e.g., as can be distinguished through dentition), there is growing evidence to suggest that the diets of South American herbivores were more generally dependent upon which plants were available (e.g., González-Guarda et al., 2018). For example, França et al. (2015) found a general trend $\delta^{13}C$ in Brazilian Pleistocene megafauna from north to south: C_4 grazing in the northern Cerrado (inferred to reflect the high abundance of C_4 grasses here at this time), to mixed feeding in the middle Cerrado, to C_3 feeding in the southern Cerrado, and then back to mixed feeding in southern Brazil, Uruguay, and northern Argentina—largely independent of which taxon was sampled. This means that in order to more completely understand the dynamics between megafaunal extirpation and vegetation, a finer spatial resolution needs to be analyzed (e.g., finer than that in this study), ideally with stable isotope analyses on the taxa in question.

The LAD of the ground sloths included in this study falls near the southern Brazil extirpation date maximum of 12,656 Cal yr BP. Most of the ground sloth samples included in this study are from southern Brazil, and their LAD coincided with a maximum in *Araucaria* forest pollen, a decline in Cerrado tree pollen, and an increase in Cerrado herbaceous pollen. It is unknown whether ground sloths ate *Araucaria* tissues, but the C₃ and mixed feeding habits of ground sloths and vegetation changes in this region, respectively, do not suggest that a loss of available forage or habitat caused the ground sloth extirpation here. Likewise, all of the *Toxodon* samples in this study

were from southern Brazil. If vegetation in southern Brazil changed such that C_3/C_4 plant ratios in the environment became too skewed, a mixed feeder such as *Toxodon* may have been driven to extirpation. The declines in grass and *Araucaria* forest pollen in this area coincide with the *Toxodon* LADs, but given there are only three *Toxodon* dates in this study, that means that these pollen declines also coincide with the *Toxodon* FADs, so whether vegetation change caused *Toxodon* extirpation cannot be determined here.

Archaeological considerations

Brazilian Pleistocene megafauna coexisted with humans for a long time. Goldberg, Mychajliw, & Hadly (2016) found that the density of Brazilian archaeological sites largely remained relatively low and constant until 5,000-4,000 Cal yr BP. This prehistoric Brazilian site density is also much lower than that of other South American regions—namely Peru, the northern Chilean coast, and the Southern Cone. However, Goldberg, Mychajliw, & Hadly (2016) also note that the general paucity of Brazilian archaeological sites at this time might be more of a taphonomic artifact due to low preservation potential in the Amazon and Atlantic Rainforests, and hence might underestimate the relative size of human populations. Evidence of human foraging within the Amazon Rainforest has been reported to date as far back as ~13,000 Cal yr BP (Roosevelt, 2013), and recent evidence suggests squash (*Cucurbita* sp.) cultivation in the Amazon Rainforest of Bolivia starting ~10,850 Cal yr BP (Lombardo et al., 2020). This highlights the need for further exploration of the Pleistocene peopling of the Amazon Rainforest—a large and important part of the Brazilian paleoecological story.

Conclusion

My data reject the hypothesis that megafaunal extirpation caused vegetation change, with the possible exception of a Caatinga tree pollen decline that postdates the extirpation window by ~200 yr. My second hypothesis—that vegetation change and subsequent habitat loss caused the megafaunal extirpation—is rejected by the Caatinga and Atlantic Rainforest pollen records, but may be consistent with changes in Cerrado and Atlantic Rainforest pollen records that precede the megafaunal extirpation estimate. The hypothesis that climate change caused the extirpation can be rejected for northern Brazil, but may be consistent with a wetting event that followed significant drying in southern Brazil from ~13,000 to ~11,500 Cal yr BP. My data do not reject the hypothesis that anthropogenic pressures caused the extirpation through direct and indirect pressures that reduced megafauna populations over millennia, but do reject a rapid "blitzkrieg" event.

The timing of extirpation in Brazil is mostly coeval with that for Pampean and Patagonian Pleistocene megafauna, but is much younger than that for Peru. Climate change is the leading hypothesis for megafaunal extirpation in the Pampas (Barnosky et al., 2016) and Peru (Rozas-Dávila et al., 2016) but a combination of humans, climate, and vegetation change are all implicated in the extirpation of megafauna from Patagonia (Villavicencio et al., 2015), I also found that humans, climate, and vegetation change correlate with Brazilian Pleistocene megafaunal extirpation, but in the form of gradual human population growth, regional effective moisture changes, and regional vegetation change.

Chapter 3: The effects of temperature and humidity on *Sporormiella minima* growth: Implications for historic and prehistoric records

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Abstract

A growing number of studies use the *Sporormiella* indicator to reconstruct historic and prehistoric populations of large terrestrial herbivores, but little is known about how sensitive this indicator is to environmental variables, including climate. In this study, I tested the following hypotheses: 1) *Sporormiella* has optimal growth rates at moderate temperatures; and 2) *Sporormiella* has maximum growth rates at high relative humidities. To test these hypotheses, I conducted experiments using *Sporormiella minima*—a *Sporormiella* species commonly reported in large terrestrial herbivore population reconstruction studies—, cultured it in growth chambers with constant temperatures and relative humidities, and recorded daily mycelial growth rates.

I found that *S. minima* grew optimally at 30 °C but did not differ in its growth between high (~100%) and low (89-95%) relative humidity treatments. Also, although the *S. minima* in this study formed hyphae and ascocarps under constant light, it did not eject spores. For temperature, a contrast between presumably optimum growth substrate temperature and ambient temperatures could inhibit *Sporormiella*'s fitness and subsequent representation in historic and prehistoric records. Relative humidity above 89% may not affect *Sporormiella*'s growth directly, but high relative humidity buffers growth media against temperature swings and effective moisture as a product of relative humidity likely still has taphonomic consequences for *Sporormiella* representation. Both variables could be complicated by local adaptation in *Sporormiella* strains and populations, making comparative work necessary to understand these factors more generally. Lastly, comparing these results with

findings from paleoecological studies highlights the potential influence of paleoclimate on *Sporormiella* growth and subsequent abundance in sediment records.

Introduction

Large terrestrial herbivores are ecologically important. As ecosystem engineers (Jones, Lawton & Shachak, 1994), they substantially increase nutrient transport rates (Doughty et al., 2016), affect the distributions of other species (Estes et al., 2011), and have a pronounced influence on atmospheric methane concentrations—with considerable implications for global warming (Solomon et al., 2007). These phenomena are well documented for modern large terrestrial herbivores, but were likely even more important prior to the Late Quaternary extinction (LQE) event. This event occurred ~50-3 ka and resulted in the loss of ~65% of all large (mass > 44 kg) mammal species worldwide (Nogues-Bravo et al., 2010). The LQE was abnormal compared to background extinction rates of large animals throughout the Cenozoic (Alroy, 1999) and peaked during an age of global climate change—including glacial-interglacial cycles throughout the Pleistocene along with warming after the last glacial maximum (LGM) (Clark et al., 2009)—and human population expansion (Brook & Barnosky, 2009). The ability to quantify large terrestrial herbivore abundances through time is key for understanding their effects on ecosystems, the dynamics of the LQE, and how to better conserve the last large terrestrial herbivores left.

One increasingly popular approach (see Baker, Bhagwat, & Willis, 2013) to reconstruct past abundances of large terrestrial herbivores is to measure relative quantities of spores from the dung fungus Sporormiella (syn: Preussia, Kruys & Wedin, 2009) in historic and prehistoric sediment records (e.g., Burney, Robinson, & Burney, 2003; Robinson, Burney, & Burney, 2005; Gill et al., 2009; Wood et al., 2011; and Rule et al., 2012). Sporormiella (Family Sporormiaceae) is an ascomycete that generally grows and reproduces on the dung of large terrestrial herbivores (Ahmed & Cain, 1972). Regarding mammals, it has been found on mammoth (Aptroot & van Geel, 3006), savanna elephant (Ebersohn & Eicker, 1997), cow, goat, sheep, donkey, horse, moose, elk, deer, rabbit, and rodent dung (Ahmed & Cain, 1972). It can also be found on moa (Wood & Wilmshurst, 2016), partridge, pheasant, and goose dung (Ahmed & Cain, 1972) though, so it is not solely adapted to mammals. Most of the > 60 species of Sporormiella (Ahmed & Cain, 1972) have only been found on dung, but S. minima, Preussia africana, P. mediterranea, and P. terricola are also known to grow on vegetation, while S. subticinensis, P. fleischhakii, P. flanaganii, P. aemulans, and P. funiculata can use soil as a growth substrate (Kruys & Wedin, 2010). Sporormiella has been found in boreal and deciduous forests (Davis & Shafer, 2006), tropical (Basumatary & McDonald, 2017) and temperate grasslands (Gill et al., 2013), and tropical forests (Harvey et al., 2019) as a wide-ranging fungus. After growing vegetatively on dung for approximately six weeks (Asina, Jain, & Kain, 1977a), the fruiting bodies (ascocarps) of Sporormiella eject spores (ascospores) that adhere to nearby vegetation (Bell, 1983) or are ultimately incorporated into soils (e.g., Wood & Wilmshurst, 2011), wetlands (e.g., Schofield & Edwards, 2011), lake sediments (e.g., Etienne et al., 2012), and nearshore marine sediments (e.g., Byrne et al., 1982). When they germinate in the new dung to repeat the cycle (Bell, 2005). Those that are preserved in sediment records are commonly applied in general paleoenvironmental studies because they have been found on every continent except Antarctica (Baker, Bhagwat, & Willis, 2012), are relatively easy to identity (Gill, 2013), and are thought to be mostly obligate to the dung of large terrestrial herbivores (Gill, 2013). *Sporormiella* hyphae have not been found in the fossil record, but *Sporormiella* spores have relatively thick, chitinous, melanized, cell walls which are thought to aid in preservation (van Asperen, Kirby, & Hunt, 2016)—the oldest record of which is from a 12 Myr-old Miocene welded tuff deposit in Idaho (Davis & Ellis, 2010). However, other environmental factors—including climate—may affect *Sporormiella*'s representation in historic and prehistoric records.

Both temperature and humidity affect *Sporormiella* ascospore germination rates (Asina, Jain, & Cain, 1977a) and ascocarp production (Asina, Jain, & Cain, 1977b). Therefore, (paleo)climatic changes and ambient weather conditions may significantly influence spore production, spore ejection, and hence spore influx rates into depositional environments and sediment records. This is important because the key assumption behind *Sporormiella*'s utility is that the quantity of *Sporormiella* spores in historic and prehistoric records is predominantly a function of how much large terrestrial herbivore dung is on the surrounding landscape, which is ultimately dependent upon how many large terrestrial herbivores are present.

In this study, I sought to test how temperature and relative humidity affect *Sporormiella* abundances, with implications for reconstructing past large terrestrial herbivore abundances. I hypothesized that: 1) *Sporormiella* has optimal growth rates at moderate temperatures; and 2) at relatively high humidities (between 89-100%), *Sporormiella* has maximum growth rates at higher humidities. To test these hypotheses, I cultured *S. minima*—a *Sporormiella* species commonly reported in large terrestrial herbivore population reconstruction studies (e.g., Davis, 1987)—on potato dextrose agar (PDA) in growth chambers set to fixed temperatures with saturated salt solutions to control relative humidities (see Rockland, 1960). I used saturated salt solutions because they are a cost-effective and well-calibrated way to control relative humidity within a closed environment.

Methods

I started by ordering four unique strains of *Sporormiella* from the United States Department of Agriculture (USDA) Agricultural Research Service (ARS) Culture Collection, Mold Database on 26 November 2019 (Table 5). These strains are available free-of-cost from the USDA ARS Northern Regional Research Laboratory (NRRL) in Peoria, IL (https://nrrl.ncaur.usda.gov/). I then stored them in the dark for five days at ~2 °C before sampling. During this time, I prepared BD DifcoTM PDA following the manufacturer's instructions, and poured 25 mL of PDA per 100 mm X 15 mm polystyrene Petri dish (hereafter "Petri dish(es)") using serological pipettes in a Baker E6-6252 laminar flow hood.

Table 5: Sporormiella strains ordered from the United States Department of Agriculture (USDA) Agricultural Research Service (ARS) Culture Collection, Mold Database, with associated collecting and growth conditions.

29987	29282	38181	66943	NRRL
				G. C.
MYC-745	MYC-467	MYC-1508	ATCC (American Type Culture Collection) 16014	Other reported number
⁷ 45	.67	508	Can Can Iture on)	er er
Sporormiella minima	Sporormiella leporina	Sporormiella minimoides	Sporormiella minima	Strain name
Donald T. Wicklow	Donald T. Wicklow	Unknown	Shung-Chang Jong	Collector
Growing on preexisting tissue of Stereum	Growing on a preexisting black stroma (possibly that of <i>Hyaxylon</i>) on downed hardwood	Unknown	Unknown	Isolation information
A mixed hardwood forest in Warm	Delabar State Park, Henderson County, IL, USA	Unknown	Unknown	Isolation locality
25	25	25	25	Reported optimal growth temperature [°C]
PDA	PDA	PDA	PDA	Original prepared growth medium

complicatum on Spring, GA, downed USA hardwood

As a pilot experiment, I placed initial isolates into plastic, 2.5 L Decor Tellfresh® Pastry Storer containers (hereafter "containers") with the container lids sealed to test which of the four strains under which lighting and general humidity conditions would grow well enough for my main temperature X relative humidity experiment. The pilot experiment was done in Conviron PGR15 growth chambers (hereafter "growth chambers") with: 1) full, fluorescent light, constantly on, measured with a LI-COR LI-250A Light Meter (average = 65.054 μmol of photons m⁻² s⁻¹, see Supplemental Table 1) vs. complete darkness; and 2) growth in ambient humidity vs. high humidity (expected value of 100%), the latter condition created by adding double-distilled water to open Petri dishes placed within the containers. I used a marker on each sample's Petri dish lid to trace daily mycelial growth at roughly the same time of day for one week, and found that S. minima strain NRRL 66943 grew the quickest of the four strains and grew quickest under full light at ambient humidity. Using full light for my primary experiment was optimal because Sporormiella does not develop pigmentation without light (Asina, Jain, & Cain, 1977b), which would have made observing and recording growth rates much more difficult. Also, I only used fluorescent lighting for this experiment, as Asina, Jain, & Cain, (1977b) found that Sporormiella ascocarp development does not require incandescent light.

Using *S. minima* strain NRRL 66943, I sampled the Petri dish from the pilot experiment with the most vigorous growth using a ~1 cm diameter cork borer and inoculated new PDA plates in a Baker UBM-400 biosafety cabinet—prepared as noted above. The cork borer was pressed vertically through the inside edge of the mycelial growth margin and each "plug" of mycelium + PDA was placed at the center of each new PDA plate for inoculation. After one week of growth, the best growing treatment was sampled by cork borer in the same way to inoculate autoclaved crystallizing glass dishes that each had 20 mL of PDA. The crystallizing dishes then had their glass lids sealed using MicroporeTM surgical tape to close them off from other microbes but allow for gas exchange. I then placed the crystalizing dishes into the containers and placed those into 2.5 gallon zipper-sealed plastic bags before placing each container in its respective growth chamber.

Sporormiella spore germination (Asina, Jain, & Cain, 1977a) and ascocarp production rates (Asina, Jain, & Cain, 1977b) have not been observed outside of 10-40 °C, so I set the growth chambers in this study to constant values of 10, 20, 30, and 40 °C. Also, Sporormiella spore germination is highest with freestanding water (near 100% relative humidity), and had not previously been known to occur at relative humidities lower than 92% (Kuthubutheen & Webster, 1986a). At 10-40 °C, a potassium nitrate saturated salt solution will create relative humidities from 89-95%, respectively (Rockland, 1960) (Table 6). As using potassium nitrate creates relative humidities on the lower end of the known Sporormiella tolerance spectrum, I therefore used potassium nitrate saturated salt solutions prepared in open Petri dishes alongside freestanding double-distilled water in open Petri dishes to create eight unique temperature × relative humidity treatment combinations, with two dishes (one replicate) per treatment. For the potassium nitrate treatments, this meant the relative humidities were expected to be 95.16% at 10 °C, 94.62% at 20 °C, 92.31% at 30 °C, and 89.03% at 40 °C (Table 6). This also meant that there was only one relative humidity per each temperature

treatment. I also included one Lascar Electronics EL-USB-2 temperature, humidity, and dew point data logger per treatment to record temperatures and relative humidities over the entire observation period (Supplemental Figs 1-8).

Table 6: Expected relative humidities for potassium nitrate at the temperatures tested in this study. All standing water treatments have expected humidity values of 100% at all temperatures.

Temperature [°C]	Expected humidity [%]	Expected humidity uncertainty [Ŧ, %]
10	95.1	1.4
20	94.6	0.66
30	92.3	0.60
40	89.0	1.2

To document *S. minima* mycelial growth rates and spore ejection, I removed each crystalizing dish from its plastic bag treatment daily at around the same time and then photographed each sample for six weeks (see Supplemental Folder 1 for photograph files) using a Motorola g⁷ cell phone camera running Android v. 9 placed at a fixed position over the edge of a 17.5 cm tall cardboard box (see Appendix 1 for camera and photograph file details). The box and dish to be photographed were placed in the same location with the same lighting to keep photograph light levels consistent while imaging. I chose a six week period because Asina, Jain, & Cain (1977a) found that maximum spore ejection rates required that long of an incubation period. I also periodically checked the samples for ascocarp development and spore ejection using a dissecting microscope. Sporormiella creates ~250 µm pseudothecial ascocarps that can be easily distinguished from a surrounding mycelial stroma (e.g., Kruys, 2015). After finishing photographing, I then used the "Selection Tool" in Adobe Photoshop 2020 to calculate ratios of how many pixels in each photograph showed mycelial coverage vs. how many pixels made up the bottom of each crystalizing dish. To standardize the daily growth selection process, I only selected areas in each photograph that had a distinct contact between hyphal cover and fresh agar—the margin of the mycelium. I then used these ratios to calculate growth rates as percentages of plate coverage per each day, with one replicate per treatment (Fig. 8).

Results and Discussion

Temperature and humidities achieved

Temperatures recorded were within ~3 °C of the programmed range for each experimental setup (10, 20, 30, and 40 °C; see Supplemental Figs 1-8). The humidity values for all treatments were lower than expected (95.16% at 10 °C, 94.62% at 20 °C, 92.31% at 30 °C, and 89.03% at 40 °C), but all of the potassium nitrate treatments were less humid than their freestanding water counterparts. The humidity values for the freestanding water treatments were within ~5% of the expected 100% relative humidity values and did not notably vary over the observation period (Supplemental Figs 1-8). However, the 10 °C potassium nitrate treatment was the only one that retained its humidity throughout the experiment. Although the other potassium nitrate treatments lost humidity throughout and at different rates, this did not seem to have any observable effects on growth rates compared to the constant humidity, freestanding water treatments at the same temperatures. This suggests that even with the heterogeneous relative humidities of the potassium nitrate treatments, these relatively lower humidities did not affect growth rates. Lastly, the data logger results show notable, punctuated daily temperature and humidity changes due to my photographing sessions where I needed to remove the samples from their growth chambers; however, they otherwise show mostly constant trends (Supplemental Figures 1-8).

Effects of temperature on Sporormiella minima growth

In general, the mycelial growth rates of the *Sporormiella minima* samples in this study were comparable between replicates, optimal at 30 °C, and absent at 40 °C (Fig. 8).

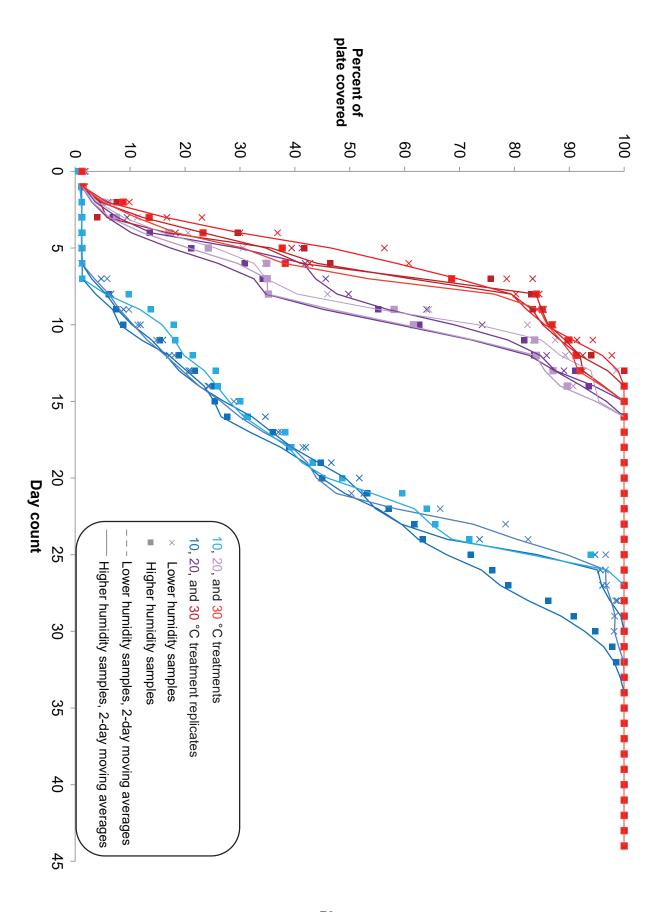


Figure 8: Growth rates of *Sporormiella minima* by day per each Plate 1 temperature X relative humidity treatment. Percent of plate covered refers to how much of each crystalizing dish showed visible mycelial growth. The 40 °C samples are not shown here because they did not grow. Growth varied notably between temperature treatments but not relative humidity treatments.

Although I did not test growth at 5 °C increments, the optimum I observed at 30 °C follows the observation from the USDA ARS NRRL that the *S. minima* strain in this study (NRRL 66943, ATCC 16014) grows optimally at 25 °C (Table 5). Asina, Jain, & Cain (1977a) found that *S. minima* germinates optimally at 30 °C, but they also found that *S. minima* produces a maximum mycelial mass anywhere from 15-40 °C (1977b). Wicklow & Moore (1974) likewise found that *S. minima* germination occurred anywhere from 10-37.5 °C, and that coprophilous ascomycete development in general was slower at cooler temperatures. It is not surprising then that the 10 °C samples in this study grew more slowly and that the 40 °C samples did not grow whatsoever. An important consideration for this experiment though is that constant temperature is not very representative of growth conditions in the field. An experiment with daily temperature oscillations may produce a different and more representative growth response.

Effects of relative humidity on Sporormiella minima growth

Coprophilous fungal growth rates are typically well known to decline in drier conditions (Kuthubutheen & Webster, 1986a), which makes the similarity between high and low relative humidity growth rates in this study quite interesting. Kuthubutheen & Webster (1986b) recorded growth rates of coprophilous fungi and found that they do not fruit at relative humidities lower than 98%; however, *Sporromiella* was not one of the fungi they investigated. The *S. minima* in this study did fruit though, suggesting that it has a relatively wide relative humidity tolerance.

As with constant temperature though, constant relative humidity is a simplification compared to field growth conditions. An experiment with a gradual reduction in relative humidity to represent aging, drying feces may be a better model to test *Sporormiella* growth (Schlüz & Shumiloskikh, 2017). Relative humidity is also not the same as effective moisture, rainfall, or overland flow, which are known to affect organic microfossil deposition (Holmes, 1994). However, high relative humidity is a prerequisite for effective moisture and rainfall, so it could have taphonomic consequences later on.

Sporormiella spore ejection and ambient light

The fact that none of the samples in this study ejected their spores is also quite interesting, as the spores are the main units of paleoecological interest (see references in the Introduction). The reproductive structures observed in this study were verified to be ascocarps and not asexual conidiophores (see Asgari & Rasoul, 2010 for *Sporormiella* conidiophores), meaning that sexual

reproduction had occurred, but the spores may not have been present within the ascocarps. Asina, Jain, & Cain (1977a) found that maximum spore ejection (no other spore ejection values were reported) occurred after their *Sporormiella* samples were incubated in six weeks of darkness, followed by a 12-hour window of full light conditions. This suggests that in field conditions, *Sporormiella* grows deep enough within dung boluses to be persistently shielded from light, and needs dung that is not disturbed and exposed to light by rainfall, scavenging insects, herbivore trampling, or other factors in order to eject spores. Once the mycelium has developed enough, *Sporormiella* then needs a cue to develop ascocarps and spores at the dung surface.

Local climatic adaptation could also affect Sporormiella levels

Local adaptation of *S. minima* may mean that strains from different areas could have different responses to temperature and relative humidity regimes. This complicates comparing the responses of modern *Sporormiella* to *Sporormiella* that grew during the last glacial maximum in boreal forest biomes, for example. The *S. minima* strain used in this study (NRRL 66943) does not have locality information associated with it, so no speculation can be made regarding adaptations to its environment of origin. The strain in this study may be specifically adapted to the area it came from and not be representative of general *Sporormiella minima* growth. One approach to address *Sporormiella* temperature and humidity adaptations could be to test for genetic markers of heat and humidity (in)tolerance, as has been done regarding thermal adaptation in *Candida albicans*—the yeast that causes thrush in humans (Leach et al., 2012).

In situ factors that could affect Sporormiella growth

Sporormiella growth could also be limited if the dung it is growing on erodes before the fungus is old enough to develop and eject spores. In a temperate conifer forest plantation in southwestern Japan, Hirata et al. (2008) found that cattle dung takes ~100-500 days to decompose to ~50-66% of its original mass, which is surprisingly slow. However, Hirata et al. (2008) note that their study plantation may have been relatively dry, and that areas with higher precipitation could have quicker dung weathering rates. Indeed, a study by Cruz et al. (2012) found that dung weathering rates in a tropical grassland in Mexico were quicker during the rainy season. Hirata et al. (2008) also noted though that an absence of dung-decomposing animals may have been responsible for the slow weathering rates they observed. In an experimental study, Horgan (2005) found that dung beetles in the eastern slopes of the Peruvian Andes removed 50-100% of pig dung samples within three days. In an experimental study on moose dung fungal diversity vs. its natural habitat in Sweden, Nyberg & Persson (2002) found that insect damage was negatively correlated with dung fungal diversity too. In sum, both high precipitation and insect damage could hinder Sporormiella growth by prematurely weathering and eroding dung, which would ultimately result in lower Sporormiella spore quantities in sediment records.

Contrasts between dung, soil, and air temperatures could also affect *Sporormiella* growth. Ashcroft & Gollan (2013) found that for soil and adjacent ground-level air samples, moisture content and the high heat capacity of water effectively buffers both soil and ground-level air from temperature swings. Air temperature was found to be more sensitive to changes in relative humidity while soil temperature depended more on vapor pressure deficit, meaning that soil requires both low humidity and high temperature to dry out and hence be more susceptible to temperature swings. At lower relative humidities, ground-level air temperature was found to be significantly correlated with topographic exposure and canopy cover, while the same held true for soils with higher vapor pressure deficits. For marked changes in ground-level and soil temperatures throughout the Quaternary (e.g., the Pleistocene - Holocene transition), this means that less humid areas would have been more susceptible to temperature swings which could have limited *Sporormiella* growth. Based on the findings in this study, this means that it is reasonable to expect that global Quaternary paleoclimatic changes could have affected ground-level microclimates and therefore could have significantly affected historic and prehistoric *Sporormiella* quantities.

Implications for interpreting paleoecological records

Changes in Quaternary (paleo) climates occur at millennial, centennial, and decadal scales, with effects that cannot be observed with diurnal time scale experiments such as this one. However, persistent temperature differences could affect *Sporormiella* growth over multiple lifecycles, which could add up to (paleo) climate timescales if those temperature differences are large enough. Table 7 shows how paleoclimate and vegetation change—a factor that could affect local microclimates—correlate with *Sporormiella* declines in select paleoecological studies.

In their study on Pleistocene *Sporormiella* declines coinciding with the formation of novel plant communities in the eastern US, Gill et al. (2009) noted that the lowering of *Sporormiella* abundances coincided with a date from a butchered mammoth bone in nearby southeastern Wisconsin. They suggest that the *Sporormiella* decline was due to a decline in large herbivore populations, and that it may have been at least partially anthropogenic. Thus, although *Sporormiella* declined in that study alongside Bølling-Allerød warming, it is consistent with the data to suggest that both climate change and large herbivore losses could have caused that *Sporormiella* decline. Gill et al. (2009) also found that *Sporormiella* decline coincided with a transition from spruce to broadleaf forest. This may also mean that large herbivore dung became more shaded by denser canopies. Nyberg & Persson (2002) found that moose dung fungal diversity was lower on dung in a spruce forest compared to a pine forest, and suggested that higher shade from the spruce branches and hence increased relative humidity was the reason. If canopy cover became greater in eastern US broadleaf forests than it was with spruce forests, the *Sporormiella* decline observed by Gill et al. (2009) coincident with this forest transition could have been at least partially due to a canopy-mediated microclimate effect as well.

Parker & Williams (2011) sought to test which factors explain *Sporormiella* quantities in modern sediments and found that county-level cattle population density and precipitation were significant predictors. They also found that precipitation was interestingly negatively correlated with *Sporormiella* spore abundance, and posited that the aerial spores could be knocked down by rainfall and therefore hindered from dispersing further. This highlighted how rainfall and precipitation could affect the dispersal and transport of *Sporormiella* spores. This is a separate mechanism from how relative humidity could affect *Sporormiella* growth, as I tested in this study. Further work is required to investigate how precipitation in a more confined experimental setting, or conversely, how relative humidity in a larger field study, could affect *Sporormiella* taphonomy.

Davis & Shafer (2006) found a correlation between *Sporormiella* declines and a transition to warm-dry conditions. This could then mean that the decline was in part due to climate change. In the Peruvian Andes, Rozas-Davila, Valencia, & Bush (2016) reported *Sporormiella* declines that coincided with warmer and wetter conditions. The warmer conditions were more generally related to post-LGM warming and the wetter conditions were inferred from an increase in benthic diatom abundances. Again, this could mean that *Sporormiella* levels lowered because they were being dispersal-limited by rainfall, but Rozas-Davila, Valencia, & Bush (2016) suggested that perhaps nearby soils became too waterlogged for palatable plants, causing a loss of food supply and subsequent large terrestrial herbivore declines.

In southeastern Brazil, Raczka, Bush, & De Oliveira (2018) observed that Sporormiella declines coincided with cooler and wetter conditions, but did not provide a mechanistic explanation for how that climatic transition would have affected *Sporormiella* quantities or large herbivore populations. In southern Patagonia, Musotto, Bianchinotti, & Borromei (2012) did not go into much detail regarding why Sporormiella quantities declined alongside a transition from forest to steppe conditions, but this could have been due to more general drying conditions. For Australia, both Rule et al. (2012) and van der Kaars et al. (2017) reported no link between Pleistocene Sporormiella declines and climate change. Rule et al. (2012) noted a coincident increase in grass and sclerophyll pollen, but argued that this was a consequence, not a cause of large terrestrial herbivore losses as inferred from Sporormiella declines. van der Kaars et al. (2017) reported a decrease in "herbaceous woody" taxa—predominantly from Asteraceae and Chenopodiae—in southwestern Australia and argued that this was due to regional drying. This means that the drying could have reduced *Sporormiella* quantities both directly at ground level and indirectly through a reduction in canopy cover, perhaps alongside large herbivore extinctions. Lastly, Robinson, Burney, & Burney (2005) did not report on the climatic conditions surrounding Holocene herbivore extinctions in Madagascar. They observed an increase in graminoid and other charcoal types, but this happened after Sporomiella declined.

The relationship between climate change and *Sporormiella* declines in sediment records is therefore not unidirectional and as many authors have pointed out (e.g., Cook et al., 2011; Feranec et al., 2011; Parker & Williams, 2011; Dodson & Field, 2018; Perrotti & van Asperen, 2019; and references therein) likely depends on many different factors. All of this is not to say that *Sporormiella* quantities are not influenced by large herbivore concentrations—there are many verification studies

to suggest that they are (e.g., Etiennne et al., 2012; Gill et al., 2013; Baker et al., 2016)—but more that the hypothesis that climate change causes *Sporormiella* quantity changes in sediment records cannot be rejected.

Conclusion

My first hypothesis was that *Sporormiella minima* grows optimally at medium temperatures. This is supported given the fastest *S. minima* mycelial growth rates occurred at 30 °C and were lower at temperatures outside of that (Fig. 8). My second hypothesis was that *Sporormiella* grows best at high humidities (approaching 100%), which is rejected given the mycelial growth rates I observed in *S. minima* were not notably different between relative humidity treatments as low as 89% (Fig. 8). Lastly, although I set out to test *Sporormiella* spore ejection rates as well, my samples did not eject spores whatsoever.

The temperature optimum for *S. minima* observed in this study matches that for previous studies on *S. minima* ascospore germination (Asina, Jain, & Cain, 1977a) and ascocarp production rates (Asina, Jain, & Cain,, 1977b). However, the insensitivity to humidity I observed in this study differs from other experimental studies that have observed humidity preferences in *S. minima* (e.g., Kuthubutheen & Webster, 1986a; 1986b). Local climatic adaptation might complicate comparing my findings to *Sporormiella* from other locations and times. However, while a handful of paleoecological studies on *Sporormiella* declines have found at least some correlation with climate change, others found no correlation. There is also a pronounced effect of moisture on soil and ground-level air temperature (Ashcroft & Gollan, 2013), meaning that paleo-humidity is likely important for buffering *Sporormiella* growth from detrimental temperature swings. This highlights the need for further work to assess the relative importance of paleoclimate—including paleotemperature, paleo-precipitation, and paleo-humidity—alongside large herbivore population reconstructions to better understand the *Sporormiella* indicator and its utility.

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Appendix 1: Archaeological localities and dates for Brazil.

Date ID	Dataset	Latitude, longitude	Radiocarbon age ∓ 1σ (yr BP)	2σ calibrated age range (Cal yr BP)	Calibration curve
an_sh_0004	ANTIGUA	-19, -43	140, 40	1 - 153	shcal13
an_sh_0020	ANTIGUA	unknown, unknown	2970, 170	2923 - 3230	shcal13
an_sh_0021	ANTIGUA	-15.4667, -56.8	2710, 60	2705 - 2949	shcal13
gb_sh_0001	Goldberg, Mychajliw, & Hadly, 2016	unknown, unknown	3775, 130	3718 - 4436	shcal13
gb_sh_0002	Goldberg, Mychajliw, & Hadly, 2016	-24.15, -46.9	4636, 100	4971 - 5488	shcal13
gb_sh_0003	Goldberg, Mychajliw, & Hadly, 2016	-24.0003, -46.4339	4520, 130	4829 - 5472	shcal13
gb_sh_0004	Goldberg, Mychajliw, & Hadly, 2016	-7.78923, -35.5813	2200, 80	1996 - 2343	shcal13
gb_sh_0005	Goldberg, Mychajliw, & Hadly, 2016	-11.1149, -42.0863	2712, 60	2707 - 2950	shcal13
gb_sh_0006	Goldberg, Mychajliw, & Hadly, 2016	-29.4167, -53.25	2945, 85	2842 - 3255	shcal13
gb_sh_0007	Goldberg, Mychajliw, & Hadly, 2016	-21.3295, -52.2104	2760, 60	2744 - 2955	shcal13
gb_sh_0008	Goldberg, Mychajliw, & Hadly, 2016	-21.3295, -52.2104	9370, 70	10288 - 10709	shcal13
gb_sh_0009	Goldberg, Mychajliw, & Hadly, 2016	-21.3295, -52.2104	10405, 100	11824 - 12451	shcal13

gb_sh_0022	gb_sh_0021	gb_sh_0020	gb_sh_0019	gb_sh_0018	gb_sh_0017	gb_sh_0016	gb_sh_0015	gb_sh_0014	gb_sh_0013	gb_sh_0012	gb_sh_0011	gb_sh_0010
Goldberg, Mychajliw, & Hadly, 2016												
-22.5429, -42.8051	-22.5429, -42.8051	-15.4667, -56.8	-25.0441, -48.5725	-8.93958, -38.7382	-30.5014, -56.2819	-30.5014, -56.2819	-11.2616, -42.0184	-11.2616, -42.0184	-11.2616, -42.0184	-11.2616, -42.0184	-11.2616, -42.0184	-11.2616, -42.0184
3540,70	3530, 30	3600, 60	5310, 50	2780, 170	8370, 60	8270, 70	9650, 90	9610, 90	9450, 90	9390, 90	8860, 115	8790, 80
3587 - 3931	3682 - 3856	3451 - 4295	5922 - 6185	2376 - 3251	9135 - 9474	9019 - 9406	10697 - 11203	10655 - 11186	10375 - 10879	10252 - 10785	9560 - 10180	9543 - 9953
shcal13												

gb_sh_0035	gb_sh_0034	gb_sh_0033	gb_sh_0032	gb_sh_0031	gb_sh_0030	gb_sh_0029	gb_sh_0028	gb_sh_0027	gb_sh_0026	gb_sh_0025	gb_sh_0024	gb_sh_0023
Goldberg, Mychajliw, & Hadly, 2016												
-8.854, -42.6078	-13.73, -44	-27.7944, -48.5445	unknown, unknown	-24.1342, -46.9189	-22.6047, -42.9569	-22.6047, -42.9569	-22.6047, -42.9569	-25.0181, -48.0514	-25.0181, -48.0514	-7.8009, -35.5759	-7.8009, -35.5759	-22.5429, -42.8051
3800, 70	8865, 110	2670, 90	2840, 60	4630, 140	3460, 70	3340, 70	2800, 60	4175, 100	3790, 110	4769, 90	4758, 90	3800, 40
3920 - 4300	9582 - 10183	2432 - 2951	2766 - 3065	4951 - 5585	3479 - 3850	3377 - 3694	2751 - 3001	4406 - 4875	3828 - 4427	5284 - 5652	5280 - 5645	3977 - 4249
shcal13												

gb_sh_0049	gb_sh_0048	gb_sh_0047	gb_sh_0045	gb_sh_0044	gb_sh_0043	gb_sh_0042	gb_sh_0041	gb_sh_0040	gb_sh_0039	gb_sh_0038	gb_sh_0037	gb_sh_0036
Goldberg, Mychajliw, & Hadly, 2016												
-22.9259, -42.547	-22.9259, -42.547	-22.9259, -42.547	-24.9047, -48.1207	-24.9047, -48.1207	-24.9047, -48.1207	-28.8, -50.49	-8.854, -42.6078	-8.854, -42.6078	-15.4667, -56.8	-8.854, -42.6078	-8.854, -42.6078	-8.854, -42.6078
4300, 190	4160, 180	3800, 190	9050, 100	4920, 100	4145, 212	6620, 175	9540, 170	7350, 180	7010, 70	6420, 120	5200, 80	4920, 70
4287 - 5323	4140 - 5065	3627 - 4629	9764 - 10412	5447 - 5774	4070 - 5083	7155 - 7797	10371 - 11217	7755 - 8442	7557 - 8074	6999 - 7509	5715 - 6126	5464 - 5753
shcal13												

gb_sh_0062	gb_sh_0061	gb_sh_0060	gb_sh_0059	gb_sh_0058	gb_sh_0057	gb_sh_0056	gb_sh_0055	gb_sh_0054	gb_sh_0053	gb_sh_0052	gb_sh_0051	gb_sh_0050
Goldberg, Mychajliw, & Hadly, 2016												
-24.9833, -47.8833	-24.9683, -47.8844	-22.8198, -42.961	-8.644, -42.3808	-8.644, -42.3808	-8.62, -43.363	-8.62, -43.363	-8.62, -43.363	-8.62, -43.363	-8.62, -43.363	-8.62, -43.363	-8.62, -43.363	-22.9259, -42.547
4120, 110	3080, 55	3760, 190	9850, 120	9700, 120	10530, 110	9730, 140	9650, 100	9160, 170	7730, 140	5090, 110	3480, 100	4520, 190
4287 - 4850	3066 - 3378	3566 - 4583	10768 - 11627	10656 - 11265	12023 - 12666	10586 - 11396	10672 - 11213	9730 - 10714	8190 - 8792	5584 - 6014	3453 - 3930	4783 - 5589
shcal13												

gb_sh_0075	gb_sh_0074	gb_sh_0073	gb_sh_0072	gb_sh_0071	gb_sh_0070	gb_sh_0069	gb_sh_0068	gb_sh_0067	gb_sh_0066	gb_sh_0065	gb_sh_0064	gb_sh_0063
Goldberg, Mychajliw, & Hadly, 2016												
-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-24.9678, -47.8519	-24.9678, -47.8519	-24.9833, -47.8833
8170, 80	8170, 90	8080, 120	8050, 170	7750, 80	7640, 160	7230, 80	7220, 80	6160, 130	6150, 50	3220, 90	3090, 110	4160, 100
8767 - 9310	8747 - 9320	8591 - 9280	8454 - 9309	8357 - 8647	8021 - 8775	7912 - 8177	7847 - 8173	6670 - 7279	6849 - 7162	3163 - 3613	2924 - 3479	4404 - 4866
shcal13												

gb_sh_0089	gb_sh_0088	gb_sh_0086	gb_sh_0085	gb_sh_0084	gb_sh_0083	gb_sh_0082	gb_sh_0081	gb_sh_0080	gb_sh_0079	gb_sh_0078	gb_sh_0077	gb_sh_0076
Goldberg, Mychajliw, & Hadly, 2016												
-25.1453, -48.0325	-25.1453, -48.0325	-25.1453, -48.0325	-25.1453, -48.0325	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556	-8.85, -42.5556
4140, 50	4060, 50	3760, 50	3750, 50	13989, 167	10454, 114	10400, 180	10050, 80	10040, 80	9800, 60	9506, 135	8600, 60	8450, 80
4511 - 4822	4385 - 4646	3904 - 4184	3894 - 4163	16378 - 17421	11937 - 12647	11599 - 12672	11241 - 11819	11240 - 11803	11070 - 11290	10386 - 11181	9457 - 9675	9239 - 9541
shcal13												

gb_sh_0102	gb_sh_0101	gb_sh_0100	gb_sh_0099	gb_sh_0098	gb_sh_0097	gb_sh_0096	gb_sh_0095	gb_sh_0094	gb_sh_0093	gb_sh_0092	gb_sh_0091	gb_sh_0090
Goldberg, Mychajliw, & Hadly, 2016												
unknown, unknown	-28.4283, -48.8294	unknown, unknown	-25.0147, -47.9267	-25.0147, -47.9267	-23.2867, -49.5139	-15.4667, -56.8	-23.2867, -49.5139	-23.2867, -49.5139	-3.7611, -49.565	-3.755, -49.6219	-25.1453, -48.0325	-25.1453, -48.0325
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5640 - 5750	3972 - 5079	1725 - 2182	2768 - 4419	3168 - 5470	7677 - 7944	5645 - 5915	4566 - 4872	4143 - 4440	10555 - 10879	10649 - 11130	4956 - 5469	4796 - 5308
shcal13												

gb_sh_0115	gb_sh_0114	gb_sh_0113	gb_sh_0112	gb_sh_0111	gb_sh_0110	gb_sh_0109	gb_sh_0108		gb_sh_0106	gb_sh_0105	gb_sh_0104	gb_sh_0103
Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajiw, & Hadly, 2016											
-22.9588, -43.0476	-23.4812, -48.267	-23.4812, -48.267	-8.825, -42.5744	-8.825, -42.5744	-19.5333, -44.0667	-23.3596, -46.7536	-23.3596, -46.7536	-23.3596, -46.7536	-23.3596, -46.7536	-23.3596, -46.7536	-25.1686, -47.9914	-25.1686, -47.9914
2328, 135	4650, 170	2060, 230	9480, 170	7610, 80	9500, 200	3370, 160	3310, 150	3230, 155	3210, 150	2270, 100	4715, 95	4630, 50
2007 - 2717	4851 - 5646	1424 - 2498	10276 - 11173	8197 - 8522	10245 - 11218	3167 - 3982	3140 - 3885	2990 - 3731	2960 - 3722	1994 - 2490	5257 - 5597	5049 - 5194
shcal13	shcal13											

gb_sh_0128	gb_sh_0127	gb_sh_0126	gb_sh_0125	gb_sh_0124	gb_sh_0123	gb_sh_0122	gb_sh_0121	gb_sh_0120	gb_sh_0119	gb_sh_0118	gb_sh_0117	gb_sh_0116
Goldberg, Mychajliw, & Hadly, 2016												
-24.8466, -48.239	-24.8466, -48.239	-28.407, -49.11	-28.407, -49.1115	-24.855, -47.475	-24.855, -47.475	-24.855, -47.475	-24.855, -47.475	-25.1323, -47.9324	-25.1323, -47.9324	-22.9588, -43.0476	-22.9588, -43.0476	-22.9588, -43.0476
8500, 70	6090, 40	3500, 50	3370, 70	4340, 110	4300, 140	3780, 110	3710, 140	5730, 60	5620, 60	7958, 224	4475, 160	2562, 139
9302 - 9545	6777 - 7009	3584 - 3855	3386 - 3721	4566 - 5085	4492 - 5088	3827 - 4422	3681 - 4413	6387 - 6637	6277 - 6493	8342 - 9333	4783 - 5475	2305 - 2894
shcal13												

gb_sh_0144	gb_sh_0143	gb_sh_0142	gb_sh_0140	gb_sh_0138	gb_sh_0137	gb_sh_0136	gb_sh_0135	gb_sh_0134	gb_sh_0133	gb_sh_0132	gb_sh_0130	gb_sh_0129
Goldberg, Mychajliw, & Hadly, 2016												
-21.3859, -44.0801	-21.3859, -44.0801	-21.3859, -44.0801	-28.4414, -48.9603	-10.136, -48.437	-10.136, -48.437	-10.136, -48.437	-24.8466, -48.239	-24.8466, -48.239	-24.8466, -48.239	-24.8466, -48.239	-24.8466, -48.239	-24.8466, -48.239
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2348 - 2771	2300 - 2752	2285 - 2722	3971 - 4237	11075 - 11404	10396 - 10755	9881 - 10234	4960 - 5312	4958 - 5292	5588 - 5798	10244 - 10510	9658 - 10165	9543 - 9964
shcal13												

gb_sh_0159	gb_sh_0158	gb_sh_0157	gb_sh_0156	gb_sh_0155	gb_sh_0154	gb_sh_0153	gb_sh_0152	gb_sh_0151	gb_sh_0150	gb_sh_0148	gb_sh_0147	gb_sh_0145
Goldberg, Mychajliw, & Hadly, 2016												
-19.5219, -44.0019	-19.5219, -44.0019	-19.5219, -44.0019	-19.521, -44.003	-23.8833, -46.3839	-19.528, -44.0367	-21.3859, -44.0801	-21.3859, -44.0801	-21.3859, -44.0801	-21.3859, -44.0801	-21.3859, -44.0801	-21.3859, -44.0801	-21.3859, -44.0801
9020, 120	8240, 40	8230, 50	6470,60	4300, 180	7970, 40	3875, 125	3400, 150	3370, 110	3350, 150	3300, 150	3275, 125	3040, 50
9682 - 10412	9021 - 9286	9009 - 9295	7247 - 7463	4377 - 5319	8627 - 8818	3863 - 4574	3229 - 3984	3340 - 3858	3171 - 3925	3137 - 3868	3156 - 3731	3004 - 3277
shcal13												

gb_sh_0172	gb_sh_0171	gb_sh_0170	gb_sh_0169	gb_sh_0168	gb_sh_0167	gb_sh_0166	gb_sh_0165	gb_sh_0164	gb_sh_0163	gb_sh_0162	gb_sh_0161	gb_sh_0160
Goldberg, Mychajliw, & Hadly, 2016												
-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-25.6721, -49.1249	-25.6721, -49.1249	-19.5219, -44.0019	-19.5219, -44.0019
4590, 100	4515, 115	4460, 100	3650, 115	3450, 100	3450, 160	2900, 95	2620, 90	2025, 95	3705, 130	2670, 80	9720, 128	9130, 60
4946 - 5470	4837 - 5332	4829 - 5317	3607 - 4244	3442 - 3910	3328 - 4091	2764 - 3231	2376 - 2847	1707 - 2159	3688 - 4359	2460 - 2929	10651 - 11326	10158 - 10433
shcal13												

gb_sh_0185	gb_sh_0184	gb_sh_0183	gb_sh_0182	gb_sh_0181	gb_sh_0180	gb_sh_0179	gb_sh_0178	gb_sh_0177	gb_sh_0176	gb_sh_0175	gb_sh_0174	gb_sh_0173
Goldberg, Mychajliw, & Hadly, 2016												
-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539
8100, 135	7820, 150	7300, 140	7152, 140	6900, 135	6820, 190	6630, 125	6600, 150	6225, 125	6085, 120	5935, 135	5603, 100	5600, 130
8588 - 9315	8325 - 9011	7826 - 8374	7658 - 8201	7484 - 7951	7307 - 7978	7262 - 7675	7161 - 7703	6748 - 7329	6638 - 7183	6401 - 7028	6179 - 6574	6168 - 6645
shcal13												

gb_sh_0199	gb_sh_0198	gb_sh_0197	gb_sh_0196	gb_sh_0195	gb_sh_0194	gb_sh_0193	gb_sh_0192	gb_sh_0191	gb_sh_0190	gb_sh_0188	gb_sh_0187	gb_sh_0186
Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016										
unknown, unknown	unknown, unknown	-28.5137, -49.0081	-28.5137, -49.0081	-28.5137, -49.0081	-28.5137, -49.0081	-28.5137, -49.0081	-28.5137, -49.0081	-28.5137, -49.0081	-22.9798, -42.0288	-18.2853, -43.8539	-18.2853, -43.8539	-18.2853, -43.8539
4070, 220	2120, 220	3350, 85	3270, 200	3165, 55	2835, 95	2740, 70	2705, 85	2115, 50	4190, 130	11000, 250	9520, 160	8400, 200
3866 - 5056	1562 - 2542	3360 - 3727	2926 - 3929	3179 - 3454	2748 - 3161	2716 - 2993	2651 - 2976	1914 - 2159	4287 - 4979	12384 - 13378	10372 - 11200	8703 - 9787
shcal13	shcal13	shcal13	shcal13	shcal13	shcal13							

gb_sh_0214	gb_sh_0213	gb_sh_0212	gb_sh_0211	gb_sh_0210	gb_sh_0208	gb_sh_0206	gb_sh_0205	gb_sh_0204	gb_sh_0203	gb_sh_0202	gb_sh_0201	gb_sh_0200
Goldberg, Mychajliw, & Hadly, 2016												
-15.4667, -56.8	unknown, unknown	unknown, unknown	-28.5487, -49.0537	-28.5518, -49.0628	-23.8435, -46.3566	-23.8435, -46.3566	-22.8282, -42.0801	-22.8282, -42.0801	-22.8282, -42.0801	-22.8282, -42.0801	-22.8282, -42.0801	-19.5381, -43.951
9460, 90	8115, 80	3350, 135	3180, 50	3640, 50	4210, 90	2590, 80	4265, 75	4205, 111	3720, 90	3215, 90	3010, 80	10460, 60
10501 - 10785	8695 - 9152	3215 - 3887	3210 - 3464	3814 - 4011	4434 - 4869	2363 - 2774	4527 - 4893	4411 - 4973	3814 - 4291	3159 - 3612	2924 - 3359	12031 - 12438
shcal13												

gb_sh_0229	gb_sh_0228	gb_sh_0227	gb_sh_0226	gb_sh_0225	gb_sh_0224	gb_sh_0221	gb_sh_0220	gb_sh_0219	gb_sh_0218	gb_sh_0217	gb_sh_0216	gb_sh_0215
Goldberg, Mychajliw, & Hadly, 2016												
unknown, unknown	-25.52, -42.472	unknown, unknown	-25.1321, -48.8804	-25.1321, -48.8804	-25.05, -48.05	-26.3014, -48.8439	-28.6157, -48.9149	-28.6157, -48.9149	-28.624, -48.9157	-28.624, -48.9157	-28.624, -48.9157	unknown, unknown
4350, 250	2010, 75	3960, 100	4124, 27	3655, 26	3490, 80	2220, 240	4420, 50	4320, 40	4290, 50	4160, 50	3930, 50	2030, 155
4236 - 5489	1731 - 2096	4076 - 4628	4508 - 4653	3835 - 3989	3545 - 3910	1692 - 2753	4841 - 5066	4808 - 4970	4782 - 4892	4517 - 4827	4150 - 4439	1606 - 2325
shcal13												

gb_sh_0243	gb_sh_0242	gb_sh_0241	gb_sh_0240	gb_sh_0239	gb_sh_0238	gb_sh_0237	gb_sh_0236	gb_sh_0235	gb_sh_0234	gb_sh_0233	gb_sh_0231	gb_sh_0230
Goldberg, Mychajliw, & Hadly, 2016												
-26.2997, -48.5684	-26.2997, -48.5684	-26.2997, -48.5684	-26.2997, -48.5684	-26.2997, -48.5684	-26.2997, -48.5684	-26.2997, -48.5684	-26.2997, -48.5684	-28.6518, -48.9741	-24.1379, -51.9939	-24.1379, -51.9939	-24.1379, -51.9939	-20, -44
5270, 80	4910, 55	4330, 140	3940, 140	3815, 50	3618, 130	2320, 55	2240, 70	4240, 190	4610, 60	3620, 60	2110, 120	4670, 130
5874 - 6211	5569 - 5733	4516 - 5299	3960 - 4709	3976 - 4299	3556 - 4247	2148 - 2433	2044 - 2345	4235 - 5305	5037 - 5333	3696 - 4006	1805 - 2339	4959 - 5600
shcal13												

gb_sh_0258	gb_sh_0257	gb_sh_0256	gb_sh_0255	gb_sh_0254	gb_sh_0253	gb_sh_0252	gb_sh_0251	gb_sh_0250	gb_sh_0249	gb_sh_0248	gb_sh_0247	gb_sh_0244
Goldberg, Mychajliw, & Hadly, 2016												
-28.5541, -48.7886	-28.5538, -48.7877	-8.13333, -36.3667	-8.13333, -36.3667	-8.13333, -36.3667	-8.13333, -36.3667	-25.5869, -54.4105	-25.5869, -54.4105	-25.5869, -54.4105	-25.5869, -54.4105	-25.5869, -54.4105	-25.5869, -54.4105	-26.2997, -48.5684
4400, 60	3090, 70	11060, 90	9150, 70	9150, 140	8495, 70	6910, 75	6505, 105	6265, 80	4035, 150	2850, 60	2035, 70	5520, 120
4829 - 5069	3023 - 3400	12727 - 13058	10169 - 10497	9885 - 10608	9299 - 9544	7578 - 7856	7230 - 7566	6908 - 7312	4080 - 4847	2765 - 3076	1809 - 2148	5985 - 6500
shcal13												

gb_sh_0272	gb_sh_0271	gb_sh_0270	gb_sh_0269	gb_sh_0268	gb_sh_0266	gb_sh_0265	gb_sh_0264	gb_sh_0263	gb_sh_0262	gb_sh_0261	gb_sh_0260	gb_sh_0259
Goldberg, Mychajliw, & Hadly, 2016												
-16.1805, -51.9911	-16.166, -52.0024	-16.166, -52.0024	-16.1609, -52.002	-17.381, -48.6676	-22.779, -41.9044	unknown, unknown	unknown, unknown	-28.6137, -48.8926	-28.6137, -48.8926	-28.6137, -48.8926	-28.6137, -48.8926	-28.5447, -48.7964
4455, 115	4100,65	2920, 75	4560, 150	2280, 60	5150, 110	5270, 300	5230, 350	4110, 70	3780, 70	2840, 70	2705, 240	4530, 70
4810 - 5325	4415 - 4730	2837 - 3215	4838 - 5488	2094 - 2353	5606 - 6029	5317 - 6659	5213 - 6730	4418 - 4821	3886 - 4299	2757 - 3077	2296 - 3365	4951 - 5314
shcal13												

gb_sh_0286	gb_sh_0285	gb_sh_0284	gb_sh_0283	gb_sh_0281	gb_sh_0280	gb_sh_0279	gb_sh_0278	gb_sh_0277	gb_sh_0276	gb_sh_0275	gb_sh_0274	gb_sh_0273
Goldberg, Mychajliw, & Hadly, 2016												
-15.4667, -56.8	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477	-18.2864, -52.0477
10120, 60	10580, 115	10400, 130	9765, 75	9195, 75	9060, 65	9020, 70	8915, 115	8805, 100	8740, 90	7420, 80	7395, 80	6690, 90
11312 - 11970	12248 - 12695	11713 - 12567	11058 - 11258	10194 - 10515	9910 - 10288	9887 - 10254	9605 - 10227	9546 - 9966	9521 - 9949	8022 - 8361	8006 - 8347	7415 - 7680
shcal13												

gb_sh_0299	gb_sh_0298	gb_sh_0297	gb_sh_0296	gb_sh_0295	gb_sh_0294	gb_sh_0293	gb_sh_0292	gb_sh_0291	gb_sh_0290	gb_sh_0289	gb_sh_0288	gb_sh_0287
Goldberg, Mychajliw, & Hadly, 2016												
-30.4333, -50.5	-14.4833, -49.4667	-18.4447, -52.0369	-18.4447, -52.0369	-16.1747, -51.9156	-16.1747, -51.9156	-16.1747, -51.9156	-16.1747, -51.9156	-16.1747, -51.9156	-16.1747, -51.9156	-16.1747, -51.9156	-18.4472, -52.0055	-18.4447, -52.0004
2980, 130	10750, 300	8880, 90	8370, 85	4505, 55	3000, 50	2900, 50	2740, 60	2475, 70	2345, 55	2140, 55	10740, 85	5720, 50
2784 - 3383	11619 - 13193	9611 - 10189	9088 - 9500	4956 - 5298	2956 - 3253	2850 - 3084	2738 - 2948	2349 - 2717	2154 - 2485	1928 - 2184	12540 - 12741	6387 - 6570
shcal13												

gb_sh_0314	gb_sh_0313	gb_sh_0312	gb_sh_0310	gb_sh_0309	gb_sh_0308	gb_sh_0307	gb_sh_0306	gb_sh_0305	gb_sh_0304	gb_sh_0302	gb_sh_0301	gb_sh_0300
Goldberg, Mychajliw, & Hadly, 2016												
-6.0875, -50.12	-6.0875, -50.12	-20.4, -45.813	-6.042, -50.201	-6.042, -50.201	-6.042, -50.201	-6.042, -50.201	-19.7148, -42.9878	-6, -50	-30.4333, -50.5	-30.4333, -50.5	-30.4333, -50.5	-30.4333, -50.5
8340, 50	8119, 50	9610, 60	8140, 130	8065, 360	7925, 45	6905, 50	4380, 70	8260, 50	4790, 95	3365, 85	3300, 95	3000, 90
9128 - 9453	8760 - 9136	10704 - 11150	8627 - 9329	8150 - 9708	8576 - 8799	7592 - 7798	4812 - 5076	9021 - 9315	5285 - 5663	3372 - 3730	3237 - 3710	2916 - 3358
shcal13												

gb_sh_0327	gb_sh_0326	gb_sh_0325	gb_sh_0324	gb_sh_0323	gb_sh_0322	gb_sh_0321	gb_sh_0320	gb_sh_0319	gb_sh_0318	gb_sh_0317	gb_sh_0316	gb_sh_0315
Goldberg, Mychajliw, & Hadly, 2016												
-25.6747, -48.5082	-15.4667, -56.8	-24.9167, -47.8667	-24.9167, -47.8667	-9.42207, -40.6296	-9.42207, -40.6296	-9.42207, -40.6296	-9.42207, -40.6296	-9.42207, -40.6296	-9.42207, -40.6296	-6.04, -50.27	-6.0875, -50.12	-6.0875, -50.12
4128, 134	5110, 230	4920, 110	4310, 105	7580, 410	5280, 120	4590, 70	3630, 70	2360, 50	2200, 110	8470, 50	9000, 50	8520, 50
4220 - 4878	5592 - 6003	5446 - 5799	4520 - 5069	7606 - 9313	5740 - 6283	4968 - 5333	3692 - 4089	2291 - 2490	1871 - 2363	9393 - 9532	9913 - 10101	9409 - 9545
shcal13												

gb_sh_0341	gb_sh_0340	gb_sh_0339	gb_sh_0338	gb_sh_0337	gb_sh_0335	gb_sh_0334	gb_sh_0333	gb_sh_0332	gb_sh_0331	gb_sh_0330	gb_sh_0329	gb_sh_0328
Goldberg, Mychajliw, & Hadly, 2016												
-22.6862, -42.046	-22.6862, -42.046	-22.6811, -42.0522	-22.6936, -42.1163	-22.6936, -42.1163	-22.7035, -42.1164	-22.7035, -42.1164	-22.7035, -42.1164	-8.90566, -38.8893	-8.90566, -38.8893	-8.90566, -38.8893	-25.05, -48.0167	-25.6747, -48.5082
3740, 110	3650, 40	2820, 200	3670, 80	2060, 60	3410, 60	3210, 50	3110, 60	3250, 180	3140, 70	2900, 170	2285, 45	4220, 200
3820 - 4407	3826 - 4010	2377 - 3368	3700 - 4155	1834 - 2112	3452 - 3729	3234 - 3484	3102 - 3401	2954 - 3870	3136 - 3457	2698 - 3449	2153 - 2346	4220 - 5300
shcal13												

gb_sh_0355	gb_sh_0354	gb_sh_0353	gb_sh_0352	gb_sh_0351	gb_sh_0350	gb_sh_0349	gb_sh_0348	gb_sh_0346	gb_sh_0345	gb_sh_0344	gb_sh_0343	gb_sh_0342
Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016				
-22.9549, -44.6522	-25.1666, -47.9143	-25.1666, -47.9143	-2.60488, -44.2865	-2.60488, -44.2865	-22.8934, -41.9809	-22.8934, -41.9809	-22.9966, -41.9943	-22.8934, -41.9809	-25.4234, -48.6732	-25.4234, -48.6732	-25.4234, -48.6732	-22.6862, -42.046
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2765 - 3007	4807 - 5055	4809 - 4985	2727 - 2766	2363 - 2542	3383 - 3579	3140 - 3356	2298 - 2470	2092 - 2311	3000 - 3569	2307 - 2772	2304 - 2758	3826 - 4583
shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13

gb_sh_0369	gb_sh_0368	gb_sh_0367	gb_sh_0366	gb_sh_0365	gb_sh_0364	gb_sh_0363	gb_sh_0362	gb_sh_0361	gb_sh_0360	gb_sh_0358	gb_sh_0357	gb_sh_0356
Goldberg, Mychajliw, & Hadly, 2016												
-27.1833, -53.75	-27.1833, -53.75	-19, -43	-27.1833, -53.75	unknown, unknown	-22.9732, -43.0245	-27.2708, -52.5083	-15.4667, -56.8	-28.3965, -48.9645	-28.3965, -48.9645	-23.1314, -44.2462	-23.1314, -44.2462	-22.9549, -44.6522
8095, 90	7600, 160	7560, 110	7145, 120	6715, 135	2290, 170	5930, 140	2600, 60	5270, 60	5170, 60	2910, 90	2650, 350	3060, 40
8634 - 9146	8004 - 8664	7981 - 8609	7689 - 8166	7304 - 7793	1893 - 2731	6398 - 7029	2428 - 2779	5891 - 6191	5710 - 6000	2775 - 3235	1874 - 3514	3073 - 3350
shcal13												

gb_sh_0383	gb_sh_0382	gb_sh_0381	gb_sh_0380	gb_sh_0379	gb_sh_0378	gb_sh_0377	gb_sh_0376	gb_sh_0375	gb_sh_0374	gb_sh_0373	gb_sh_0371	gb_sh_0370
Goldberg, Mychajliw, & Hadly, 2016												
-28.5615, -48.9827	-28.5615, -48.9827	-28.5615, -48.9827	-28.5615, -48.9827	-29.5275, -53.584	unknown, unknown	-25.8833, -47.8833	-25.8833, -47.8833	-25.8833, -47.8833	-24.8667, -47.8833	-24.8667, -47.8833	-27.1833, -53.75	-27.1833, -53.75
4185, 90	3995, 85	2655, 110	2430, 125	2190, 80	3270, 70	5245, 125	5070, 100	4685, 105	3635, 90	3900, 100	8640, 95	8640, 180
4433 - 4853	4147 - 4643	2360 - 2929	2152 - 2749	1994 - 2339	3329 - 3633	5710 - 6221	5588 - 5948	5038 - 5593	3681 - 4149	3970 - 4529	9432 - 9898	9243 - 10181
shcal13												

gb_sh_0396	gb_sh_0395	gb_sh_0394	gb_sh_0393	gb_sh_0392	gb_sh_0391	gb_sh_0390	gb_sh_0389	gb_sh_0388	gb_sh_0387	gb_sh_0386	gb_sh_0385	gb_sh_0384
Goldberg, Mychajliw, & Hadly, 2016												
-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603
2280, 80	2270, 75	2240, 170	2210, 60	2180, 105	2170, 45	2170, 95	2165, 75	2115, 65	2075, 65	2070, 60	2060, 85	2020, 40
2011 - 2381	2037 - 2358	1831 - 2623	2038 - 2325	1891 - 2348	2004 - 2188	1913 - 2340	1986 - 2318	1888 - 2183	1833 - 2155	1864 - 2151	1785 - 2161	1836 - 2009
shcal13												

gb_sh_0410	gb_sh_0409	gb_sh_0408	gb_sh_0407	gb_sh_0406	gb_sh_0405	gb_sh_0404	gb_sh_0403	gb_sh_0402	gb_sh_0401	gb_sh_0400	gb_sh_0399	gb_sh_0398
Goldberg, Mychajliw, & Hadly, 2016												
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2795, 35	2655, 105	2500, 155	2490, 35	2470, 55	2370, 35	2365, 45	2345, 105	2340, 50	2335, 35	2320, 50	2310, 70	2295, 90
2768 - 2945	2362 - 2895	2148 - 2866	2358 - 2549	2351 - 2621	2303 - 2471	2296 - 2490	2083 - 2623	2156 - 2440	2295 - 2360	2149 - 2379	2084 - 2468	2008 - 2491
shcal13												

gb_sh_0424	gb_sh_0422	gb_sh_0421	gb_sh_0420	gb_sh_0419	gb_sh_0418	gb_sh_0417	gb_sh_0416	gb_sh_0415	gb_sh_0414	gb_sh_0413	gb_sh_0412	gb_sh_0411
Goldberg, Mychajliw, & Hadly, 2016												
-9.597, -37.8661	-25.0846, -48.0197	-25.0846, -48.0197	-25.0846, -48.0197	-25.0846, -48.0197	-25.0846, -48.0197	-23.3284, -52.7633	-23.3284, -52.7633	-24.6333, -47.7022	-28.6033, -49.0215	-28.579, -48.9603	-28.579, -48.9603	-28.579, -48.9603
2500, 10	5010, 115	4970, 110	4380, 100	4350, 110	4130, 100	6683, 355	5241, 306	5240, 150	3080, 80	2890, 55	2880, 75	2855, 105
2376 - 2545	5468 - 5943	5463 - 5915	4796 - 5295	4570 - 5093	4382 - 4849	6731 - 8184	5288 - 6673	5649 - 6285	2990 - 3404	2842 - 3083	2779 - 3163	2747 - 3211
shcal13												

gb_sh_0437	gb_sh_0436	gb_sh_0435	gb_sh_0434	gb_sh_0433	gb_sh_0432	gb_sh_0431	gb_sh_0430	gb_sh_0429	gb_sh_0428	gb_sh_0427	gb_sh_0426	gb_sh_0425
Goldberg, Mychajliw, & Hadly, 2016												
-11.9074, -52.9384	-28.543, -49.0748	-9.75, -48.3716	-19.6355, -43.8773	-19.6355, -43.8773	-28.5347, -48.7879	-28.5303, -48.7871	-28.5314, -48.7885	-28.5367, -48.7904	-3.27962, -45.1403	-9.597, -37.8661	-9.597, -37.8661	-9.597, -37.8661
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7753 - 7955	6091 - 6318	11750 - 12176	7936 - 8170	7431 - 7577	1834 - 2063	4491 - 4728	4403 - 4652	4797 - 4976	2457 - 2718	9762 - 10221	4830 - 4879	3138 - 3734
shcal13												

gb_sh_0450	gb_sh_0449	gb_sh_0448	gb_sh_0447	gb_sh_0446	gb_sh_0445	gb_sh_0444	gb_sh_0443	gb_sh_0442	gb_sh_0441	gb_sh_0440	gb_sh_0439	gb_sh_0438
Goldberg, Mychajliw, & Hadly, 2016												
-19.516, -44.0675	-19.516, -44.0675	-19, -43	-19.516, -44.0675	-19.516, -44.0675	-19, -43	-19.516, -44.0675	-19.516, -44.0675	-19.516, -44.0675	-19, -43	-27.1833, -53.75	-19.516, -44.0675	-11.9074, -52.9384
8810, 60	8750, 150	8730, 110	8510, 60	8420, 100	8360, 50	8300, 50	8280, 50	8240, 50	8190, 40	7560, 160	7500, 60	8040, 40
9552 - 9949	9479 - 10181	9492 - 9956	9397 - 9547	9119 - 9539	9194 - 9465	9084 - 9423	9030 - 9326	9010 - 9305	9002 - 9150	8152 - 8544	8169 - 8392	8701 - 9009
shcal13												

gb_sh_0463	gb_sh_0462	gb_sh_0461	gb_sh_0460	gb_sh_0459	gb_sh_0458	gb_sh_0457	gb_sh_0456	gb_sh_0455	gb_sh_0454	gb_sh_0453	gb_sh_0452	gb_sh_0451
Goldberg, Mychajliw, & Hadly, 2016												
-19.8167, -43.95	-19.55, -43.9928	-19.6525, -44.011	-19.6525, -44.011	-19.516, -44.0675	-19.516, -44.0675	-19.516, -44.0675	-19.516, -44.0675	-19.516, -44.0675	-19.516, -44.0675	-19.516, -44.0675	-19.516, -44.0675	-19, -43
9350, 80	8830, 50	8520, 40	7870, 40	12240, 50	10150, 130	9650, 60	9640, 50	9600, 60	9420, 60	9210, 130	8980, 60	8820, 150
10262 - 10698	9594 - 9955	9436 - 9537	8511 - 8769	13907 - 14276	11240 - 12102	10745 - 11175	10749 - 11161	10692 - 11145	10404 - 10764	10119 - 10699	9886 - 10232	9530 - 10203
shcal13												

gb_sh_0476	gb_sh_0475	gb_sh_0474	gb_sh_0473	gb_sh_0472	gb_sh_0471	gb_sh_0470	gb_sh_0469	gb_sh_0468	gb_sh_0467	gb_sh_0466	gb_sh_0465	gb_sh_0464
Goldberg, Mychajliw, & Hadly, 2016												
-18.2853, -43.8539	-18.2853, -43.8539	-19.5916, -43.9419	-15.1166, -44.2166	-15.1166, -44.2166	-15.1166, -44.2166	-15.1166, -44.2166	-15.1166, -44.2166	-15.1166, -44.2166	-15.1166, -44.2166	-15.1166, -44.2166	-15.1166, -44.2166	-15.1166, -44.2166
10560, 40	10380, 60	9780, 70	12070, 170	12000, 300	11440, 240	11250, 150	11000, 232	10910, 140	10250, 345	10200, 250	10000, 232	9870, 260
12405 - 12569	11947 - 12422	11062 - 11269	13460 - 14474	13202 - 14934	12780 - 13714	12737 - 13325	12400 - 13338	12556 - 13063	11063 - 12725	11171 - 12570	10746 - 12174	10496 - 12113
shcal13												

gb_sh_0489	gb_sh_0488	gb_sh_0487	gb_sh_0486	gb_sh_0485	gb_sh_0484	gb_sh_0483	gb_sh_0482	gb_sh_0481	gb_sh_0480	gb_sh_0479	gb_sh_0478	gb_sh_0477
Goldberg, Mychajliw, & Hadly, 2016												
-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-15.4667, -56.8	-19.4772, -44.0392	-18.303, -43.7419	-16.2617, -46.0486	-16.2617, -46.0486	-14.45, -44.44	-14.45, -44.44	-20.2011, -55.267
4070, 60	4010, 130	3960, 40	3950, 40	3930, 40	3830, 90	3810, 50	10210, 60	9580, 200	8595, 215	11000, 300	10000, 255	2200, 50
4380 - 4660	4086 - 4828	4230 - 4445	4227 - 4440	4220 - 4423	4066 - 4298	3972 - 4298	11600 - 12046	10252 - 11291	9080 - 10175	12059 - 13430	10734 - 12319	2040 - 2311
shcal13												

gb_sh_0503	gb_sh_0502	gb_sh_0501	gb_sh_0500	gb_sh_0498	gb_sh_0497	gb_sh_0496	gb_sh_0495	gb_sh_0494	gb_sh_0493	gb_sh_0492	gb_sh_0491	gb_sh_0490
Goldberg, Mychajliw, & Hadly, 2016												
-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-15.4667, -56.8	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392
8580, 50	8540, 50	8530, 40	8230, 40	8170, 50	7940, 70	7890, 40	7700, 40	7400, 40	5990, 40	4470, 40	4290, 90	4140, 40
9442 - 9564	9432 - 9547	9443 - 9539	9019 - 9275	8979 - 9276	8591 - 8814	8538 - 8780	8387 - 8542	8037 - 8224	6670 - 6889	4868 - 5080	4520 - 5046	4513 - 4729
shcal13												

gb_sh_0517	gb_sh_0515	gb_sh_0514	gb_sh_0513	gb_sh_0512	gb_sh_0511	gb_sh_0510	gb_sh_0509	gb_sh_0508	gb_sh_0507	gb_sh_0506	gb_sh_0505	gb_sh_0504
Goldberg, Mychajliw, & Hadly, 2016												
-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392
8800, 40	8790, 40	8750, 40	8730, 50	8710, 40	8710, 80	8700, 40	8690, 40	8670, 40	8660, 50	8620, 40	8600, 50	8600, 160
9557 - 9912	9560 - 9901	9546 - 9799	9538 - 9798	9537 - 9736	9493 - 9914	9534 - 9706	9532 - 9701	9528 - 9688	9497 - 9699	9481 - 9631	9465 - 9631	9192 - 9954
shcal13												

gb_sh_0530	gb_sh_0529	gb_sh_0528	gb_sh_0527	gb_sh_0526	gb_sh_0525	gb_sh_0524	gb_sh_0523	gb_sh_0522	gb_sh_0521	gb_sh_0520	gb_sh_0519	gb_sh_0518
Goldberg, Mychajliw, & Hadly, 2016												
-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392
9470, 50	9370, 40	9150, 40	9100, 40	8980, 40	8930, 40	8900, 40	8890, 40	8880, 50	8870, 100	8840, 60	8820, 40	8810, 90
10508 - 10788	10398 - 10683	10196 - 10305	10163 - 10287	9913 - 10205	9885 - 10186	9762 - 10168	9736 - 10161	9701 - 10159	9595 - 10187	9600 - 9965	9582 - 9934	9548 - 9963
shcal13												

gb_sh_0543	gb_sh_0542	gb_sh_0541	gb_sh_0540	gb_sh_0539	gb_sh_0538	gb_sh_0537	gb_sh_0536	gb_sh_0535	gb_sh_0534	gb_sh_0533	gb_sh_0532	gb_sh_0531
Goldberg, Mychajliw, & Hadly, 2016												
-19.5415, -43.9414	-22.05, -42.675	-19.5415, -43.9414	-19.5415, -43.9414	-19.5415, -43.9414	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392	-19.4772, -44.0392
8960, 50	8310, 40	7680, 40	7650, 50	4300, 300	10490, 50	10130, 60	10070, 100	9900, 40	9720, 40	9680, 50	9650, 50	9520, 60
9886 - 10220	9118 - 9426	8377 - 8524	8340 - 8539	4072 - 5587	12057 - 12240	11387 - 11850	11243 - 11841	11198 - 11356	11066 - 11212	10775 - 11039	10758 - 11168	10567 - 10883
shcal13												

gb_sh_0559	gb_sh_0558	gb_sh_0557	gb_sh_0556	gb_sh_0555	gb_sh_0554	gb_sh_0550	gb_sh_0549	gb_sh_0548	gb_sh_0547	gb_sh_0546	gb_sh_0545	gb_sh_0544
Goldberg, Mychajliw, & Hadly, 2016												
-19.6064, -43.7344	-19.6064, -43.7344	-19.6064, -43.7344	-19.6064, -43.7344	-19.6064, -43.7344	-19.6064, -43.7344	-19.6064, -43.7344	-15.1358, -44.2442	-15.1358, -44.2442	-15.1358, -44.2442	-15.1358, -44.2442	-15.1358, -44.2442	-15.1358, -44.2442
9620, 40	9550, 60	9540, 90	9040, 40	8910, 40	8730, 40	8080, 40	10450, 70	9500, 130	9390, 160	9140, 90	8890, 90	8640, 90
10736 - 11110	10644 - 10910	10553 - 11143	10123 - 10243	9772 - 10174	9539 - 9782	8721 - 9031	12008 - 12442	10388 - 11175	10228 - 11100	10120 - 10517	9623 - 10197	9439 - 9832
shcal13												

gb_sh_0574	gb_sh_0572	gb_sh_0571	gb_sh_0570	gb_sh_0569	gb_sh_0567	gb_sh_0566	gb_sh_0565	gb_sh_0564	gb_sh_0563	gb_sh_0562	gb_sh_0561	gb_sh_0560
Goldberg, Mychajliw, & Hadly, 2016												
-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6388, -43.976	-19.6388, -43.976	-19.6388, -43.976	-19.6388, -43.976	-19.6388, -43.976	-19.6388, -43.976
3750, 110	3720, 120	3660, 110	3580, 130	3430, 130	3260, 110	3070, 110	11990, 50	9760, 70	8810, 50	8350, 40	8290, 40	7190, 50
3823 - 4412	3700 - 4317	3631 - 4246	3478 - 4157	3354 - 3982	3158 - 3713	2921 - 3455	13591 - 13978	11061 - 11250	9554 - 9938	9194 - 9444	9081 - 9332	7845 - 8054
shcal13												

gb_sh_0588	gb_sh_0587	gb_sh_0586	gb_sh_0585	gb_sh_0583	gb_sh_0582	gb_sh_0581	gb_sh_0580	gb_sh_0579	gb_sh_0578	gb_sh_0577	gb_sh_0576	gb_sh_0575
Goldberg, Mychajliw, & Hadly, 2016												
-9.38854, -40.4572	-25.0814, -48.5684	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966	-19.6064, -43.8966
6390, 80	6980, 90	12960, 300	10200, 220	9330, 60	8490, 160	6950, 140	6830, 150	5120, 130	4550, 130	4400, 120	4350, 120	4170, 120
7154 - 7430	7614 - 7942	14243 - 16244	11206 - 12447	10267 - 10604	9012 - 9797	7554 - 8000	7424 - 7936	5587 - 6127	4844 - 5474	4783 - 5313	4568 - 5289	4292 - 4892
shcal13												

gb_sh_0602	gb_sh_0601	gb_sh_0600	gb_sh_0599	gb_sh_0598	gb_sh_0597	gb_sh_0596	gb_sh_0595	gb_sh_0594	gb_sh_0593	gb_sh_0592	gb_sh_0591	gb_sh_0590
Goldberg, Mychajliw, & Hadly, 2016												
-22.8299, -42.9226	-28.5182, -48.9707	-28.5208, -48.9687	-28.5208, -48.9687	unknown, unknown	-9.80306, -48.3936	-23.9027, -46.2048	-23.9027, -46.2048	-23.9525, -46.1847	-22.8829, -42.0001	-22.8829, -42.0001	-22.8829, -42.0001	-22.8829, -42.0001
5180, 80	4685, 160	2535, 165	2245, 60	4400, 280	9940, 60	3925, 145	3865, 95	4400, 130	5140, 180	4020, 80	3725, 75	3050, 80
5660 - 6024	4872 - 5650	2153 - 2929	2077 - 2345	4223 - 5612	11202 - 11499	3897 - 4655	3963 - 4445	4574 - 5317	5575 - 6280	4222 - 4649	3827 - 4248	2958 - 3382
shcal13												

gb_sh_0616	gb_sh_0615	gb_sh_0614	gb_sh_0613	gb_sh_0612	gb_sh_0611	gb_sh_0610	gb_sh_0609	gb_sh_0608	gb_sh_0606	gb_sh_0605	gb_sh_0604	gb_sh_0603
Goldberg, Mychajliw, & Hadly, 2016												
-6.7, -36.6	-9.6375, -48.4138	-9.6375, -48.4138	-9.6375, -48.4138	-9.6375, -48.4138	-9.6375, -48.4138	-9.6375, -48.4138	-9.6375, -48.4138	-15.7097, -44.0175	-15.8, -44.1	-21.657, -52.553	-21.657, -52.553	-21.657, -52.553
9640, 100	10530, 90	9990, 60	9890, 80	9790, 70	9670, 60	9456, 95	9397, 80	9135, 105	8845, 90	10190, 190	8620, 110	8215, 120
10660 - 11207	12057 - 12650	11229 - 11629	11104 - 11510	11064 - 11291	10760 - 11186	10376 - 10892	10268 - 10772	10111 - 10524	9583 - 10162	11228 - 12427	9371 - 9909	8760 - 9462
shcal13												

gb_sh_0630	gb_sh_0629	gb_sh_0628	gb_sh_0627	gb_sh_0625	gb_sh_0624	gb_sh_0623	gb_sh_0622	gb_sh_0621	gb_sh_0620	gb_sh_0619	gb_sh_0618	gb_sh_0617
Goldberg, Mychajliw, & Hadly, 2016												
-19.583, -52.66	-28.5362, -48.9624	-22.7853, -42.3636	-22.7853, -42.3636	-28.5026, -48.9753	-28.5026, -48.9753	-24.5629, -47.7403	-24.5629, -47.7403	-24.5629, -47.7403	-24.5629, -47.7403	-28.5094, -49.0209	-28.5094, -49.0209	-24.6847, -47.6181
10090, 70	2075, 110	2600, 160	2020, 70	4480, 60	3230, 70	5895, 45	5420, 30	4985, 35	4511, 32	3360, 70	3240, 70	4790, 115
11269 - 11830	1781 - 2213	2303 - 3007	1777 - 2096	4869 - 5145	3226 - 3575	6529 - 6786	6171 - 6282	5594 - 5747	4971 - 5292	3381 - 3717	3233 - 3582	5267 - 5735
shcal13												

gb_sh_0643	gb_sh_0642	gb_sh_0641	gb_sh_0640	gb_sh_0639	gb_sh_0638	gb_sh_0637	gb_sh_0636	gb_sh_0635	gb_sh_0634	gb_sh_0633	gb_sh_0632	gb_sh_0631
Goldberg, Mychajliw, & Hadly, 2016												
-16.793, -56.7041	-16.9507, -55.7154	-15.9216, -54.378	-15.9216, -54.378	-15.9216, -54.378	-15.9216, -54.378	-15.9216, -54.378	-15.9216, -54.378	-16.9507, -55.6165	-15.3785, -54.7266	-15.4667, -56.8	-19.583, -52.66	-19.583, -52.66
2560, 80	2570,70	10080, 80	8390, 80	8270, 80	8210, 80	8180, 80	8160, 60	2110, 65	3470, 75	2970, 50	10480, 80	10340, 110
2364 - 2751	2377 - 2754	11256 - 11832	9127 - 9521	9014 - 9422	8975 - 9420	8850 - 9314	8951 - 9278	1884 - 2181	3542 - 3876	2871 - 3253	12011 - 12559	11692 - 12437
shcal13												

gb_sh_0656	gb_sh_0655	gb_sh_0654	gb_sh_0653	gb_sh_0652	gb_sh_0651	gb_sh_0650	gb_sh_0649	gb_sh_0648	gb_sh_0647	gb_sh_0646	gb_sh_0645	gb_sh_0644
Goldberg, Mychajliw, & Hadly, 2016												
-8.902, -38.708	-5.933, -50.666	-5.933, -50.666	-25, -47.9181	-25, -47.9181	-14.4631, -48.4435	-5.95, -50.616	-5.95, -50.6	-5.966, -50.5333	-5.966, -50.5333	-24.1336, -46.9503	-16.9507, -55.858	-16.9507, -55.8582
3840, 180	8850, 40	8680, 40	4380, 160	2840, 225	10605, 125	8310, 60	8240, 90	8110, 60	8050, 70	4575, 110	2390, 60	5750, 80
3696 - 4647	9672 - 9961	9531 - 9693	4513 - 5325	2357 - 3413	12250 - 12709	9078 - 9434	8979 - 9457	8702 - 9137	8628 - 9032	4866 - 5470	2299 - 2542	6314 - 6669
shcal13												

gb_sh_0671	gb_sh_0670	gb_sh_0669	gb_sh_0668	gb_sh_0667	gb_sh_0666	gb_sh_0665	gb_sh_0664	gb_sh_0663	gb_sh_0662	gb_sh_0660	gb_sh_0658	gb_sh_0657
Goldberg, Mychajliw, & Hadly, 2016												
-7.79157, -35.5579	-8.0387, -34.9973	-8.61206, -37.1671	-8.61206, -37.1671	-8.61206, -37.1671	-8.61206, -37.1671	-8.61206, -37.1671	-24.7947, -48.1113	-27.7743, -48.516	-27.7743, -48.516	-27.7743, -48.516	-27.7743, -48.516	-24.6183, -47.7181
2266, 110	2130, 400	6640, 95	6240, 110	4390, 200	3870, 200	2780, 190	3530, 70	4515, 100	4460, 110	3850, 105	3735, 100	5035, 140
1929 - 2493	1259 - 3007	7318 - 7625	6792 - 7326	4421 - 5472	3717 - 4729	2359 - 3265	3577 - 3928	4848 - 5325	4816 - 5325	3897 - 4444	3819 - 4300	5450 - 6016
shcal13												

gb_sh_0685	gb_sh_0684	gb_sh_0683	gb_sh_0682	gb_sh_0681	gb_sh_0679	gb_sh_0678	gb_sh_0677	gb_sh_0676	gb_sh_0675	gb_sh_0674	gb_sh_0673	gb_sh_0672
Goldberg, Mychajliw, & Hadly, 2016												
-9.72283, -38.4354	-9.72283, -38.4354	-29.6522, -54.1121	-17.198, -47.6189	-17.198, -47.6189	-17.198, -47.6189	-17.198, -47.6189	-17.198, -47.6189	-17.198, -47.6189	-17.198, -47.6189	-17.198, -47.6189	-17.198, -47.6189	-7.79157, -35.5579
2709, 110	2245, 110	2795, 55	9400, 90	9400, 35	8280, 30	5790, 60	4710, 25	4160, 70	2890, 25	2860, 25	2620, 60	2802, 110
2432 - 3062	1913 - 2488	2752 - 2980	10257 - 10789	10490 - 10697	9081 - 9316	6403 - 6677	5314 - 5471	4506 - 4833	2869 - 3062	2843 - 3007	2455 - 2797	2701 - 3212
shcal13												

gb_sh_0700	gb_sh_0699	gb_sh_0698	gb_sh_0697	gb_sh_0696	gb_sh_0695	gb_sh_0694	gb_sh_0693	gb_sh_0690	gb_sh_0689	gb_sh_0688	gb_sh_0687	gb_sh_0686
Goldberg, Mychajliw, & Hadly, 2016												
-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-18.3111, -52.0369	-2.045, -54.1445	-2.045, -54.1445	-9.72283, -38.4354
10290, 70	10290, 80	10280, 70	10275, 275	10261, 62	10260, 60	10250, 70	10230, 60	10190, 50	10120, 80	10110, 60	10000, 60	2915, 130
11703 - 12180	11698 - 12315	11692 - 12172	11202 - 12678	11618 - 12105	11687 - 12093	11601 - 12118	11604 - 12064	11600 - 12022	11323 - 11849	11318 - 11835	11236 - 11643	2756 - 3275
shcal13												

gb_sh_0715	gb_sh_0714	gb_sh_0713	gb_sh_0711	gb_sh_0710	gb_sh_0709	gb_sh_0708	gb_sh_0707	gb_sh_0706	gb_sh_0705	gb_sh_0704	gb_sh_0703	gb_sh_0702
Goldberg, Mychajliw, & Hadly, 2016												
-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445
10450, 60	10392, 78	10390, 60	10390, 70	10370, 60	10360, 60	10360, 50	10350, 70	10330, 70	10330, 60	10320, 70	10310, 70	10305, 275
12018 - 12436	11926 - 12433	11964 - 12423	11938 - 12430	11943 - 12418	11934 - 12414	11944 - 12406	11912 - 12412	11802 - 12407	11814 - 12310	11767 - 12311	11756 - 12312	11228 - 12683
shcal13												

gb_sh_0730	gb_sh_0729	gb_sh_0728	gb_sh_0727	gb_sh_0726	gb_sh_0725	gb_sh_0724	gb_sh_0723	gb_sh_0722	gb_sh_0721	gb_sh_0720	gb_sh_0719	gb_sh_0717
Goldberg, Mychajliw, & Hadly, 2016												
-25.0628, -47.9242	-25.0833, -48.0167	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445	-2.045, -54.1445
3170, 95	3330, 125	11145, 135	11110, 310	10905, 295	10875, 295	10683, 80	10655, 285	10560, 60	10510, 60	10490, 80	10480, 70	10470,70
3073 - 3566	3216 - 3839	12719 - 13198	12380 - 13566	11950 - 13359	11926 - 13310	12431 - 12711	11601 - 13074	12381 - 12656	12356 - 12560	12024 - 12560	12034 - 12554	12026 - 12454
shcal13												

gb_sh_0744	gb_sh_0743	gb_sh_0741	gb_sh_0740	gb_sh_0739	gb_sh_0738	gb_sh_0737	gb_sh_0736	gb_sh_0735	gb_sh_0734	gb_sh_0733	gb_sh_0732	gb_sh_0731
Goldberg, Mychajliw, & Hadly, 2016												
-27.5922, -48.4592	-27.5922, -48.4592	-22.964, -42.0311	-23.4101, -49.2301	-24.65, -47.4833	-25.4704, -48.4803	-25.4704, -48.4803	-25.4704, -48.4803	-8.55, -36.8656	-25.06, -47.9257	-25.06, -47.9257	-25.06, -47.9257	-25.0628, -47.9242
2400, 250	2220, 250	2080, 40	3600, 160	3090, 120	4930, 100	4890, 110	4481, 110	2030, 50	3770, 70	3700, 70	3660, 70	3250, 90
1807 - 2980	1594 - 2756	1897 - 2098	3559 - 4161	2919 - 3484	5452 - 5893	5318 - 5761	4827 - 5326	1828 - 2060	3867 - 4296	3824 - 4161	3717 - 4098	3208 - 3641
shcal13												

gb_sh_0757	gb_sh_0756	gb_sh_0755	gb_sh_0754	gb_sh_0753	gb_sh_0752	gb_sh_0751	gb_sh_0750	gb_sh_0749	gb_sh_0748	gb_sh_0747	gb_sh_0746	gb_sh_0745
Goldberg, Mychajliw, & Hadly, 2016												
-15.0874, -43.1443	-15.0874, -43.1443	-15.0874, -43.1443	-15.0874, -43.1443	-15.0874, -43.1443	-22.8873, -42.5808	unknown, unknown	-23.1733, -44.2583	-1.35093, -48.829	-1.35093, -48.829	-1.35093, -48.829	-27.5922, -48.4592	-27.5922, -48.4592
4740, 80	4695, 80	4610, 55	4380, 80	4340, 235	2270, 190	3870, 100	2880, 40	4500, 90	4090, 95	3490, 195	4280, 400	3690, 100
5282 - 5602	5262 - 5587	5038 - 5333	4807 - 5090	4241 - 5477	1827 - 2742	3961 - 4449	2843 - 3076	4857 - 5314	4288 - 4831	3228 - 4249	3705 - 5736	3691 - 4255
shcal13												

gb_sh_0770	gb_sh_0769	gb_sh_0768	gb_sh_0767	gb_sh_0766	gb_sh_0765	gb_sh_0764	gb_sh_0763	gb_sh_0762	gb_sh_0761	gb_sh_0760	gb_sh_0759	gb_sh_0758
Goldberg, Mychajliw, & Hadly, 2016												
unknown, unknown	-26.9327, -48.6372	-26.9327, -48.6372	-24.0873, -54.2784	-28.5831, -49.0013	-25.2891, -48.1359	-25.2891, -48.1359	-25.2891, -48.1359	-15.0874, -43.1443	-15.0874, -43.1443	-15.0874, -43.1443	-15.0874, -43.1443	-15.0874, -43.1443
3920, 100	4990, 210	3815, 145	4065, 75	3610, 70	6030, 130	4760, 80	4540, 90	5115, 195	5070, 95	5050, 85	5045, 95	4750, 65
3982 - 4569	5275 - 6211	3718 - 4529	4287 - 4727	3687 - 4012	6504 - 7166	5288 - 5610	4863 - 5326	5461 - 6280	5590 - 5941	5596 - 5915	5584 - 5938	5316 - 5584
shcal13												

gb_sh_0783	gb_sh_0782	gb_sh_0781	gb_sh_0780	gb_sh_0779	gb_sh_0778	gb_sh_0777	gb_sh_0776	gb_sh_0775	gb_sh_0774	gb_sh_0773	gb_sh_0772	gb_sh_0771
Goldberg, Mychajliw, & Hadly, 2016												
-22.631, -42.9435	-24.4686, -47.9672	-24.4686, -47.9672	-24.4686, -47.9672	unknown, unknown	-24.4522, -47.2178	-28.5595, -49.0988	-28.5595, -49.0988	-24.0675, -46.8	-28.5133, -48.8917	unknown, unknown	unknown, unknown	unknown, unknown
3170, 70	4860, 100	4750, 110	4710, 145	3300, 100	4560, 110	6590, 60	5410, 50	5970, 140	2390, 70	4260, 210	6540, 105	5040, 90
3156 - 3484	5312 - 5748	5256 - 5652	4958 - 5658	3228 - 3721	4862 - 5336	7409 - 7569	6090 - 6280	6445 - 7033	2297 - 2546	4217 - 5321	7242 - 7582	5588 - 5920
shcal13												

gb_sh_0796	gb_sh_0795	gb_sh_0794	gb_sh_0793	gb_sh_0792	gb_sh_0791	gb_sh_0790	gb_sh_0789	gb_sh_0788	gb_sh_0787	gb_sh_0786	gb_sh_0785	gb_sh_0784
Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016							
-29.3835, -51.596	-24.1358, -46.9	unknown, unknown	unknown, unknown	-23.094, -53.5411	-26.2289, -51.0126	-29.6167, -50.2875	-29.6167, -50.2875	-29.6167, -50.2875	-15.3785, -54.7266	unknown, unknown	unknown, unknown	unknown, unknown
7800, 50	4635, 100	3030, 170	2970, 180	5380, 110	3110, 140	5950, 190	5680, 240	4280, 180	2970, 70	3550, 150	4240, 150	4400, 200
8422 - 8627	4970 - 5488	2768 - 3510	2741 - 3481	5898 - 6322	2916 - 3573	6311 - 7175	5908 - 7007	4338 - 5312	2735 - 3513	3443 - 4160	4379 - 5077	4425 - 5472
shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13

gb_sh_0809	gb_sh_0808	gb_sh_0807	gb_sh_0806	gb_sh_0805	gb_sh_0804	gb_sh_0803	gb_sh_0802	gb_sh_0801	gb_sh_0800	gb_sh_0799	gb_sh_0798	gb_sh_0797
Goldberg, Mychajliw, & Hadly, 2016												
-29.6133, -56.93	-29.6133, -56.93	-29.6133, -56.93	-29.7892, -57.075	-29.7892, -57.075	-29.7892, -57.075	-29.7181, -56.6638	-29.5126, -51.7278	-29.5126, -51.7278	-29.5126, -51.7278	-29.5126, -51.7278	-29.5126, -51.7278	-29.527, -51.7443
10240, 80	10200, 125	9620, 110	10010, 190	9840, 105	9230, 145	10810, 275	8430, 50	8150, 50	8030, 50	6180, 50	3000, 40	5655, 140
11586 - 12113	11273 - 12154	10647 - 11202	11062 - 12110	11057 - 11505	10110 - 10752	11823 - 13205	9282 - 9520	8969 - 9260	8692 - 9007	6881 - 7173	2965 - 3240	6174 - 6739
shcal13												

gb_sh_0822	gb_sh_0821	gb_sh_0820	gb_sh_0819	gb_sh_0818	gb_sh_0817	gb_sh_0816	gb_sh_0815	gb_sh_0814	gb_sh_0813	gb_sh_0812	gb_sh_0811	gb_sh_0810
Goldberg, Mychajliw, & Hadly, 2016												
-28.6117, -56.0049	-29.7892, -57.075	-29.7892, -57.075	-29.7892, -57.075	-28.9505, -56.3052	-29.287, -56.5589	-29.7371, -57.0756	-29.7797, -57.1285	-29.5322, -56.865	-29.7456, -57.048	-29.6133, -56.93	-29.6133, -56.93	-29.6133, -56.93
11555, 230	9855, 130	9595, 175	8585, 115	3525, 145	9035, 100	10180, 275	9605, 120	9450, 115	9120, 340	10985, 100	10800, 150	10400, 110
12835 - 13791	10763 - 11653	10373 - 11265	9274 - 9898	3440 - 4103	9739 - 10303	11083 - 12658	10572 - 11205	10293 - 10901	9471 - 11185	12698 - 13035	12387 - 13034	11797 - 12554
shcal13												

gb_sh_0837	gb_sh_0836	gb_sh_0835	gb_sh_0833	gb_sh_0832	gb_sh_0831	gb_sh_0829	gb_sh_0828	gb_sh_0827	gb_sh_0826	gb_sh_0825	gb_sh_0824	gb_sh_0823
Goldberg, Mychajliw, & Hadly, 2016												
-29.8038, -51.585	-29.8038, -51.585	-29.8038, -51.585	-29.7725, -50.5622	-29.7725, -50.5622	-29.7725, -50.5622	-15.4667, -56.8	-29.7725, -50.5622	-29.6854, -52.463	-32.5757, -52.428	-32.1034, -52.4761	-32.5699, -52.4322	-32.5699, -52.4322
7240, 40	6215, 30	5230, 40	7390, 40	4690, 40	4610, 140	3970, 60	3730, 60	2920, 120	2020, 50	2435, 85	2160, 80	2000, 120
7940 - 8068	6957 - 7168	5885 - 6022	8026 - 8220	5297 - 5476	4870 - 5488	4235 - 4449	3847 - 4161	2763 - 3268	1823 - 2055	2305 - 2738	1927 - 2319	1609 - 2163
shcal13												

gb_sh_0853	gb_sh_0852	gb_sh_0851	gb_sh_0850	gb_sh_0849	gb_sh_0848	gb_sh_0847	gb_sh_0846	gb_sh_0845	gb_sh_0841	gb_sh_0840	gb_sh_0839	gb_sh_0838
Goldberg, Mychajliw, & Hadly, 2016												
-22.9169, -42.5506	-22.9169, -42.5506	-29.7007, -51.9665	-29.7007, -51.9665	-29.7007, -51.9665	-29.7007, -51.9665	-22.8689, -41.9954	-22.8689, -41.9954	unknown, unknown	-29.5939, -51.7278	-29.5939, -51.7278	-29.5939, -51.7278	-29.5939, -51.7278
3280, 60	2250, 60	4885, 65	4877, 64	4859, 64	4490, 136	4490, 40	4340, 70	3540, 50	9430, 360	8290, 130	8020, 150	7250, 350
3344 - 3614	2081 - 2346	5455 - 5725	5450 - 5715	5445 - 5662	4810 - 5471	4951 - 5093	4782 - 5054	3632 - 3909	9601 - 11652	8971 - 9527	8506 - 9262	7417 - 8780
shcal13												

gb_sh_0866	gb_sh_0865	gb_sh_0864	gb_sh_0863	gb_sh_0862	gb_sh_0861	gb_sh_0860	gb_sh_0859	gb_sh_0858	gb_sh_0857	gb_sh_0856	gb_sh_0855	gb_sh_0854
Goldberg, Mychajliw, & Hadly, 2016												
-22.93, -44.3467	-22.93, -44.3467	-4.59513, -56.3281	-22.9169, -42.5506	-22.9169, -42.5506	-22.9169, -42.5506	-22.9169, -42.5506	-22.9169, -42.5506	-22.9169, -42.5506	-22.9169, -42.5506	-22.9169, -42.5506	-22.9169, -42.5506	-22.9169, -42.5506
7860, 80	3350, 80	5570, 125	4430, 65	4320, 62	4256, 62	4218, 63	4071, 73	4069, 66	4056, 73	3965, 66	3905, 67	3858, 60
8420 - 8795	3363 - 3723	5998 - 6567	4841 - 5082	4784 - 4985	4566 - 4870	4528 - 4848	4294 - 4728	4340 - 4712	4280 - 4662	4149 - 4529	4084 - 4442	4077 - 4415
shcal13												

gb_sh_0881	gb_sh_0879	gb_sh_0877	gb_sh_0876	gb_sh_0875	gb_sh_0874	gb_sh_0873	gb_sh_0872	gb_sh_0871	gb_sh_0870	gb_sh_0869	gb_sh_0868	gb_sh_0867
Goldberg, Mychajliw, & Hadly, 2016												
-30.2223, -50.3926	-22.9742, -42.4851	-22.9742, -42.4851	-25.444, -48.4551	-25.444, -48.4551	-25.444, -48.4551	-25.444, -48.4551	-25.444, -48.4551	-25.444, -48.4551	-25.444, -48.4551	-25.444, -48.4551	-25.444, -48.4551	-25.444, -48.4551
4620, 100	3960, 200	3610, 190	4970, 95	3500, 60	3496, 56	3424, 62	3373, 58	3361, 70	3344, 61	3306, 61	3284, 61	3271, 48
4960 - 5485	3827 - 4863	3445 - 4413	5569 - 5907	3572 - 3882	3574 - 3866	3463 - 3734	3441 - 3704	3381 - 3718	3388 - 3647	3366 - 3636	3348 - 3617	3359 - 3573
shcal13												

gb_sh_0897	gb_sh_0896	gb_sh_0895	gb_sh_0894	gb_sh_0893	gb_sh_0892	gb_sh_0891	gb_sh_0890	gb_sh_0889	gb_sh_0888	gb_sh_0887	gb_sh_0883	gb_sh_0882
Goldberg, Mychajliw, & Hadly, 2016												
-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-30.2223, -50.3926	-30.2223, -50.3926
3567, 27	3567, 50	3561, 53	3533, 29	3510, 36	3507, 22	3479, 38	3473, 25	3420, 61	3391, 26	3172, 33	4740, 90	4640, 80
3699 - 3891	3683 - 3930	3677 - 3928	3685 - 3859	3631 - 3845	3679 - 3831	3591 - 3829	3589 - 3732	3458 - 3732	3544 - 3645	3238 - 3413	5270 - 5609	5036 - 5482
shcal13												

gb_sh_0910	gb_sh_0909	gb_sh_0908	gb_sh_0907	gb_sh_0906	gb_sh_0905	gb_sh_0904	gb_sh_0903	gb_sh_0902	gb_sh_0901	gb_sh_0900	gb_sh_0899	gb_sh_0898
Goldberg, Mychajliw, & Hadly, 2016												
-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394
3743, 26	3740, 30	3729, 35	3720, 30	3710, 68	3692, 68	3670, 30	3662, 66	3662, 64	3660, 30	3654, 32	3620, 30	3588, 65
3962 - 4103	3957 - 4104	3901 - 4100	3897 - 4094	3828 - 4183	3822 - 4157	3840 - 4001	3811 - 4097	3813 - 4096	3835 - 3995	3831 - 3996	3820 - 3980	3676 - 3988
shcal13												

gb_sh_0924	gb_sh_0923	gb_sh_0922	gb_sh_0921	gb_sh_0920	gb_sh_0919	gb_sh_0918	gb_sh_0917	gb_sh_0916	gb_sh_0915	gb_sh_0914	gb_sh_0913	gb_sh_0911
Goldberg, Mychajliw, & Hadly, 2016												
-29.6058, -50.025	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394	-22.5278, -41.9394
3420, 60	4127, 24	4043, 26	3979, 35	3968, 31	3910, 30	3860, 40	3852, 31	3820, 40	3810, 40	3810, 30	3800, 49	3747, 62
3458 - 3732	4513 - 4652	4412 - 4533	4245 - 4447	4243 - 4441	4223 - 4414	4089 - 4359	4086 - 4300	3985 - 4295	3982 - 4259	4066 - 4244	3966 - 4295	3869 - 4238
shcal13												

gb_sh_0938	gb_sh_0937	gb_sh_0936	gb_sh_0935	gb_sh_0934	gb_sh_0933	gb_sh_0932	gb_sh_0931	gb_sh_0929	gb_sh_0928	gb_sh_0927	gb_sh_0926	gb_sh_0925
Goldberg, Mychajliw, & Hadly, 2016												
-15.4667, -56.8	-15.4667, -56.8	-24.9167, -47.8667	-23.2867, -49.5139	-29.7725, -50.5622	-19.4772, -44.0392	-23.55, -49.65	-15.4667, -56.8	-15.4667, -56.8	-22.6974, -42.9429	-22.6974, -42.9429	-22.6974, -42.9429	-29.3541, -49.7812
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6466 - 6755	6298 - 6568	5308 - 6313	5288 - 6310	4220 - 4525	3915 - 4420	3687 - 3991	2924 - 3257	2152 - 2492	3836 - 4239	3888 - 4102	3339 - 3641	3441 - 3644
shcal13												

gb_sh_0951	gb_sh_0950	gb_sh_0949	gb_sh_0948	gb_sh_0947	gb_sh_0946	gb_sh_0945	gb_sh_0944	gb_sh_0943	gb_sh_0942	gb_sh_0941	gb_sh_0940	gb_sh_0939
Goldberg, Mychajliw, & Hadly, 2016												
-16.33, -56.7638	-16.33, -56.7638	-16.33, -56.7638	-19.4772, -44.0392	-15.4667, -56.8	-8.854, -42.6078	-16.33, -56.7638	-15.4667, -56.8	-15.4667, -56.8	-15.4667, -56.8	-15.4667, -56.8	-15.4667, -56.8	-15.4667, -56.8
9340,70	9340, 20	9320, 20	7940, 50	7050, 55	7010, 170	6750, 230	6410, 60	6060, 80	6040, 70	5980, 70	5920, 70	5890, 70
10267 - 10672	10402 - 10582	10375 - 10571	8576 - 8990	7704 - 7948	7671 - 7940	7156 - 8020	7230 - 7422	6668 - 7030	6661 - 7013	6616 - 6952	6500 - 6861	6474 - 6803
shcal13												

gb_sh_0964	gb_sh_0963	gb_sh_0962	gb_sh_0961	gb_sh_0960	gb_sh_0959	gb_sh_0958	gb_sh_0957	gb_sh_0956	gb_sh_0955	gb_sh_0954	gb_sh_0953	gb_sh_0952
Goldberg, Mychajliw, & Hadly, 2016												
-28.5822, -48.8368	-28.5822, -48.8368	-28.5834, -48.8362	-28.5834, -48.8362	-28.584, -48.8228	-28.589, -48.8219	-28.5914, -48.8306	-2.045, -54.1445	-16.33, -56.7638	-16.33, -56.7638	-16.33, -56.7638	-16.33, -56.7638	-3.2, -60.3275
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4421 - 4709	1894 - 2150	2485 - 2787	2420 - 2736	4287 - 4622	5886 - 6122	3212 - 3498	11330 - 11840	11146 - 11233	11070 - 11195	10763 - 11107	10945 - 11075	10392 - 10891
shcal13												

gb_sh_0978	gb_sh_0977	gb_sh_0976	gb_sh_0975	gb_sh_0974	gb_sh_0973	gb_sh_0972	gb_sh_0971	gb_sh_0969	gb_sh_0968	gb_sh_0967	gb_sh_0966	gb_sh_0965
Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016	Goldberg, Mychajliw, & Hadly, 2016
-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-19.1284, -43.7272	-28.5849, -48.8375
9460, 110	8840, 130	8400, 300	8381, 280	8280, 40	8230, 150	8185, 110	8150, 150	7820, 60	5680, 70	5350, 60	2310, 50	3510, 50
10372 - 11098	9548 - 10183	8591 - 9967	8582 - 9950	9071 - 9322	8701 - 9484	8722 - 9423	8625 - 9424	8414 - 8715	6292 - 6567	5935 - 6215	2150 - 2358	3606 - 3869
shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13	shcal13

gb_sh_0991	gb_sh_0990	gb_sh_0989	gb_sh_0988	gb_sh_0987	gb_sh_0986	gb_sh_0985	gb_sh_0984	gb_sh_0983	gb_sh_0982	gb_sh_0981	gb_sh_0980	gb_sh_0979
Goldberg, Mychajliw, & Hadly, 2016												
-27.743, -49.1886	unknown, unknown	-25.5, -49.5	-25.5, -49.5	-25.5, -49.5	-25.5, -49.5	-19.1284, -43.7272	-19.1284, -43.7272					
3000, 120	2040, 60	4440, 50	4050, 60	4010, 50	3800, 50	2050, 50	4960, 110	4810, 100	4665, 90	4070, 105	12760, 70	11960, 250
2841 - 3394	1822 - 2103	4851 - 5073	4287 - 4648	4244 - 4539	3966 - 4295	1863 - 2091	5460 - 5911	5291 - 5731	5043 - 5493	4235 - 4832	14797 - 15369	13235 - 14674
shcal13												

gb_sh_1004	gb_sh_1003	gb_sh_1002	gb_sh_1001	gb_sh_1000	gb_sh_0999	gb_sh_0998	gb_sh_0997	gb_sh_0996	gb_sh_0995	gb_sh_0994	gb_sh_0993	gb_sh_0992
Goldberg, Mychajliw, & Hadly, 2016												
-2.46911, -54.2813	-2.46911, -54.2813	-2.46911, -54.2813	-25.0333, -47.9833	-25.0333, -47.9833	-22.8574, -42.9575	unknown, unknown	unknown, unknown	-7.79564, -35.5738	-22.6414, -42.9757	-22.6414, -42.9757	-22.6414, -42.9757	-27.1716, -53.7519
6590, 100	6300, 90	5705, 80	4010, 110	3960, 90	3200, 190	6240, 250	9040, 400	4650, 150	2510, 60	2290, 60	2160, 60	7260, 100
7266 - 7597	6944 - 7335	6300 - 6637	4144 - 4728	4083 - 4589	2917 - 3829	6503 - 7519	9190 - 11208	4872 - 5595	2360 - 2720	2094 - 2357	1994 - 2309	7837 - 8215
shcal13												

gb_sh_1017	gb_sh_1016	gb_sh_1015	gb_sh_1014	gb_sh_1013	gb_sh_1012	gb_sh_1011	gb_sh_1010	gb_sh_1009	gb_sh_1008	gb_sh_1007	gb_sh_1006	gb_sh_1005
Goldberg, Mychajliw, & Hadly, 2016												
-8.787, -42.515	-8.787, -42.515	-24.7389, -48.0273	-24.7461, -47.9644	-2.46911, -54.2813	-2.46911, -54.2813	-2.46911, -54.2813	-2.46911, -54.2813	-2.46911, -54.2813	-2.46911, -54.2813	-2.46911, -54.2813	-2.46911, -54.2813	-2.46911, -54.2813
8800, 60	8670, 60	5740, 50	3990, 70	7090, 80	7080, 80	7010, 90	7000, 80	6980, 80	6930, 80	6880, 80	6860, 100	6640, 80
9548 - 9943	9490 - 9764	6394 - 6639	4152 - 4582	7697 - 8006	7693 - 7998	7652 - 7963	7655 - 7953	7650 - 7936	7586 - 7868	7564 - 7852	7492 - 7860	7410 - 7614
shcal13												

gb_sh_1031	gb_sh_1030	gb_sh_1029	gb_sh_1028	gb_sh_1026	gb_sh_1025	gb_sh_1024	gb_sh_1023	gb_sh_1022	gb_sh_1021	gb_sh_1020	gb_sh_1019	gb_sh_1018
Goldberg, Mychajliw, & Hadly, 2016												
-8.90517, -42.6916	-11.0333, -42.1167	-11.0333, -42.1167	-11.0333, -42.1167	-11.0333, -42.1167	-11.0333, -42.1167	-11.0333, -42.1167	-8.80747, -42.8831	-8.859, -42.588	-8.859, -42.588	-8.859, -42.588	-8.86717, -43.0424	-8.86717, -43.0424
2960, 60	6450, 150	6330, 150	6030, 80	3820, 340	3570, 60	2020, 130	6990, 70	8820, 70	8190, 60	8160, 70	8700, 90	7940, 90
2872 - 3234	6967 - 7578	6841 - 7475	6636 - 7027	3329 - 5054	3677 - 3975	1695 - 2211	7660 - 7938	9555 - 9957	8977 - 9305	8847 - 9287	9478 - 9921	8537 - 9007
shcal13												

gb_sh_1046	gb_sh_1045	gb_sh_1044	gb_sh_1043	gb_sh_1041	gb_sh_1040	gb_sh_1039	gb_sh_1038	gb_sh_1037	gb_sh_1036	gb_sh_1035	gb_sh_1033	gb_sh_1032
Goldberg, Mychajliw, & Hadly, 2016												
-9.00182, -42.7628	-7.48058, -36.6847	-7.48058, -36.6847	-8.86583, -42.5858	-7.99365, -42.2199	-7.99365, -42.2199	-8.87045, -42.9886	-8.8025, -42.4169	-8.8025, -42.4169	-8.90517, -42.6916	-8.90517, -42.6916	-8.90517, -42.6916	-8.90517, -42.6916
7180, 90	3320, 60	3010, 60	10390, 80	10900, 900	2000, 300	10480, 50	9670, 140	6270, 140	4730, 110	4290, 110	3130, 50	3100, 50
7786 - 8171	3375 - 3641	2955 - 3272	11921 - 12433	10206 - 15133	1306 - 2544	12251 - 12443	10557 - 11275	6794 - 7422	5210 - 5614	4510 - 5064	3159 - 3407	3138 - 3383
shcal13												

gb_sh_1060	& Hadly, 2016	-8.1569, -42.64	9200, 40	10230 - 10430
gb_sh_1048 gb_sh_1049 gb_sh_1050	& Hadly, 2016 Goldberg, Mychajliw, & Hadly, 2016 Goldberg, Mychajliw, & Hadly, 2016 Goldberg, Mychajliw,	-9.00182, -42.7628 -9.00182, -42.7628 -9.00182, -42.7628	8080, 170 9080, 170 9700, 200	8537 - 9418 9622 - 10585 10414 - 11629
gb_sh_1051	Goldberg, Mychajliw, & Hadly, 2016 Goldberg, Mychajliw,	-11.1432, -42.1288	3230, 210	2859 - 3901
gb_sh_1052	Goldberg, Mychajliw, & Hadly, 2016	-8.844, -42.5616	10270, 35	11796 - 12046
gb_sh_1053	Goldberg, Mychajliw, & Hadly, 2016	-7.71324, -42.727	2090, 110	1802 - 2316
gb_sh_1054	Goldberg, Mychajliw, & Hadly, 2016	-8.92472, -42.6083	12210, 40	13905 - 14196
gb_sh_1055	Goldberg, Mychajliw, & Hadly, 2016	-8.738, -42.743	10400, 100	11819 - 12450
gb_sh_1056	Goldberg, Mychajliw, & Hadly, 2016	-8.738, -42.743	10570, 80	12364 - 12673
gb_sh_1057	Goldberg, Mychajliw, & Hadly, 2016	-8.738, -42.743	10800, 70	12614 - 12762
gb_sh_1058	Goldberg, Mychajliw, & Hadly, 2016	-8.1569, -42.64	2840, 100	2745 - 3179
gb_sh_1059	Goldberg, Mychajliw, & Hadly, 2016	-8.1569, -42.64	9180, 40	10219 - 10423
gb_sh_1060	Goldberg, Mychajliw, & Hadly, 2016	-8.1569, -42.64	9200, 40	10230 - 104

gb_sh_1076	gb_sh_1075	gb_sh_1072	gb_sh_1070	gb_sh_1069	gb_sh_1068	gb_sh_1067	gb_sh_1066	gb_sh_1065	gb_sh_1064	gb_sh_1063	gb_sh_1062	gb_sh_1061
Goldberg, Mychajliw, & Hadly, 2016												
-8.83917, -42.5639	-8.83917, -42.5639	-9.14715, -43.1891	-9.52972, -41.4921	-9.52972, -41.4921	-9.52972, -41.4921	-9.4051, -42.0249	-9.4051, -42.0249	-9.4051, -42.0249	-8.41667, -42.3331	-8.41667, -42.3331	-8.41667, -42.3331	-8.41667, -42.3331
9200, 60	8960, 70	8910, 50	8610, 60	7930, 30	7400, 60	7730, 60	7430, 50	7380, 50	8780, 120	8670, 120	8600, 100	7000, 100
10222 - 10497	9770 - 10226	9760 - 10178	9465 - 9682	8590 - 8788	8024 - 8327	8390 - 8588	8149 - 8343	8017 - 8222	9535 - 9975	9424 - 9955	9394 - 9821	7613 - 7964
shcal13												

gb_sh_1092	gb_sh_1091	gb_sh_1088	gb_sh_1087	gb_sh_1086	gb_sh_1085	gb_sh_1084	gb_sh_1082	gb_sh_1081	gb_sh_1080	gb_sh_1079	gb_sh_1078	gb_sh_1077
Goldberg, Mychajliw, & Hadly, 2016	& Hadly, 2016											
-22.35, -41.8167	-22.35, -41.8167	-8.8519, -41.2998	-8.88392, -42.6321	-8.85556, -42.59	-8.85556, -42.59	-8.86889, -42.613	-8.66, -42.725	-8.66, -42.725	-8.66, -42.725	-8.66, -42.725	-8.83917, -42.5639	-8.83917, -42.5639
3975, 160	3635, 135	7330, 50	6900, 70	10640, 50	9870, 50	9920, 70	8500, 60	2950, 110	2880, 100	2790, 110	12440, 230	12200, 600
3968 - 4831	3560 - 4296	7981 - 8191	7577 - 7844	12512 - 12674	11169 - 11355	11179 - 11504	9395 - 9543	2791 - 3274	2755 - 3218	2698 - 3181	13781 - 15250	12860 - 15986
shcal13	shcal13											

mc_in_0005	mc_in_0004	mc_in_0003	mc_in_0002	mc_in_0001	gb_sh_1103	gb_sh_1101	gb_sh_1100	gb_sh_1099	gb_sh_1096	gb_sh_1095	gb_sh_1094	gb_sh_1093
McMichael & Bush, 2019	Goldberg, Mychajliw, & Hadly, 2016											
-2.47, -60	-2.47, -60	-0.794, -63.097	-0.794, -63.097	-0.794, -63.097	-23.0107, -43.5767	-24.8833, -47.885	-24.8833, -47.885	-24.8692, -47.8856	-22.986, -42.0139	-22.986, -42.0139	-23.0046, -42.0033	-23.0046, -42.0033
520, 120	470, 130	1310, 30	1290, 25	1150, 25	2260, 160	4680, 110	4440, 80	4070, 100	3060, 50	2440, 40	3180, 40	2068, 31
308 - 681	275 - 685	1224 - 1294	1221 - 1284	980 - 1098	1880 - 2712	5034 - 5592	4843 - 5145	4242 - 4827	3058 - 3364	2341 - 2540	3236 - 3449	1903 - 2060
intcal13	intcal13	intcal13	intcal13	intcal13	shcal13							

mc_in_0019	mc_in_0018	mc_in_0017	mc_in_0015	mc_in_0014	mc_in_0013	mc_in_0012	mc_in_0011	mc_in_0010	mc_in_0009	mc_in_0008	mc_in_0007	mc_in_0006
McMichael & Bush, 2019												
-2.46, -60	-2.45, -60	-2.49, -60	-2.49, -60	-2.45, -60	-2.5, -60	-2.49, -60	-2.49, -60	-2.47, -60	-2.49, -60	-2.49, -60	-2.47, -60	-2.47, -60
1400, 120	1280, 120	1280, 150	1270, 120	1170, 280	1170, 120	1140, 130	1080, 140	1050, 220	980, 120	970, 140	890, 170	580, 120
1059 - 1553	953 - 1396	921 - 1424	937 - 1382	632 - 1622	901 - 1305	890 - 1293	739 - 1275	636 - 1368	684 - 1095	666 - 1181	618 - 1152	423 - 738
intcal13												

mc_in_0032	mc_in_0031	mc_in_0030	mc_in_0029	mc_in_0028	mc_in_0027	mc_in_0026	mc_in_0025	mc_in_0024	mc_in_0023	mc_in_0022	mc_in_0021	mc_in_0020
McMichael & Bush, 2019												
-1.98, -58.5	-2.15, -58.95	-1.98, -58.4	-2.45, -60	-2.45, -60	-2.45, -60	-2.45, -60	-2.48, -60	-2.48, -60	-2.5, -60	-2.48, -60	-2.45, -60	-2.49, -60
1050, 70	1040, 70	910, 60	2410, 120	1800, 190	1750, 230	1670, 140	1530, 120	1510, 190	1480, 240	1470, 160	1430, 140	1430, 130
794 - 1090	788 - 1088	724 - 931	2298 - 2751	1312 - 2151	1258 - 2182	1308 - 1874	1256 - 1709	1053 - 1829	924 - 1904	1053 - 1724	1054 - 1621	1062 - 1607
intcal13												

mc_in_0046	mc_in_0045	mc_in_0044	mc_in_0043	mc_in_0042	mc_in_0041	mc_in_0040	mc_in_0039	mc_in_0038	mc_in_0036	mc_in_0035	mc_in_0034	mc_in_0033
McMichael & Bush, 2019												
1.65, -67.3	1.8, -67.7	1.7, -67.4	-2.2, -58.55	-2.2, -58.55	-2.15, -58.95	-2.2, -58.55	-1.6, -58.55	-2.45, -58.57	-2.1, -58.55	-2.1, -58.5	-2.1, -58.5	-2.45, -58.57
260, 50	250, 60	250, 50	1800, 60	1640, 130	1490, 80	1360, 90	1320, 70	1290, 70	1240, 70	1230, 80	1200, 70	1190, 70
267 - 467	255 - 482	261 - 343	1594 - 1868	1301 - 1824	1284 - 1547	1061 - 1416	1070 - 1346	1058 - 1327	1049 - 1293	981 - 1290	976 - 1273	969 - 1268
intcal13												

mc_in_0059	mc_in_0058	mc_in_0057	mc_in_0056	mc_in_0055	mc_in_0054	mc_in_0053	mc_in_0052	mc_in_0051	mc_in_0050	mc_in_0049	mc_in_0048	mc_in_0047
McMichael & Bush, 2019												
1.6, -67.3	1.6, -67.3	1.25, -67.5	1.6, -67.3	1.25, -67.5	1.6, -67.3	1.7, -67.4	1.25, -67.5	1.05, -67.7	1.6, -67.3	1.65, -67.3	1.8, -67.7	1.05, -67.7
1100, 50	1100, 90	1040, 50	920, 90	740, 50	670, 50	640, 50	530, 50	500, 50	480, 50	430, 60	400, 80	350,70
928 - 1093	899 - 1188	899 - 1062	677 - 980	639 - 762	551 - 685	545 - 672	502 - 568	474 - 564	451 - 561	420 - 544	292 - 547	286 - 517
intcal13												

mc_in_0073	mc_in_0072	mc_in_0071	mc_in_0070	mc_in_0069	mc_in_0068	mc_in_0066	mc_in_0065	mc_in_0064	mc_in_0063	mc_in_0062	mc_in_0061	mc_in_0060
McMichael & Bush, 2019												
1.7, -67.4	1.05, -67.7	1.63, -67.45	1.65, -67.3	1.8, -67.7	1.25, -67.5	1.05, -67.7	1.7, -67.4	1.65, -67.3	1.25, -67.5	1.7, -67.4	1.7, -67.4	1.25, -67.5
1560, 60	1540, 80	1430, 60	1410, 80	1400, 140	1340, 60	1290, 80	1260, 80	1240, 50	1230, 90	1220, 80	1180, 90	1170, 50
1327 - 1564	1298 - 1571	1261 - 1419	1180 - 1424	1045 - 1570	1172 - 1367	1052 - 1344	1046 - 1305	1060 - 1282	968 - 1296	978 - 1287	951 - 1278	964 - 1185
intcal13												

mc_sh_0004	mc_sh_0003	mc_sh_0002	mc_sh_0001	mc_in_0082	mc_in_0081	mc_in_0080	mc_in_0079	mc_in_0078	mc_in_0077	mc_in_0076	mc_in_0075	mc_in_0074
McMichael & Bush, 2019												
-3.191, -60.346	-3.191, -60.346	-3.191, -60.346	-3.191, -60.346	-3.407, -64.614	-3.408, -64.562	-3.414, -64.617	-3.4, -64.6	-3.434, -64.624	-3.412, -64.562	1.6, -67.3	1.63, -67.45	1.7, -67.4
2280, 100	1800, 80	1610, 90	1590, 40	2580, 30	1970, 50	1700, 30	970, 25	470, 30	430, 25	6260, 110	2070, 80	1700, 60
1997 - 2494	1511 - 1884	1302 - 1617	1354 - 1534	2699 - 2762	1817 - 2050	1544 - 1637	796 - 875	494 - 540	462 - 523	6912 - 7420	1870 - 2186	1516 - 1740
shcal13	shcal13	shcal13	shcal13	intcal13								

mc_sh_0053	mc_sh_0052	mc_sh_0050	mc_sh_0049	mc_sh_0048	mc_sh_0047	mc_sh_0046	mc_sh_0045	mc_sh_0044	mc_sh_0043	mc_sh_0038	mc_sh_0006	mc_sh_0005
McMichael & Bush, 2019												
-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-14.555, -60.217	-3.549, -59.2	-3.549, -59.2
1070, 70	1010, 80	1000, 40	980, 40	960, 30	960, 40	910, 40	890, 120	570, 40	350, 40	2315, 54	2370, 30	1800, 40
773 - 1065	725 - 991	773 - 932	765 - 927	760 - 918	746 - 919	684 - 822	622 - 965	502 - 563	300 - 473	2147 - 2379	2305 - 2462	1571 - 1748
shcal13												

mc_sh_0067	mc_sh_0066	mc_sh_0065	mc_sh_0064	mc_sh_0063	mc_sh_0062	mc_sh_0060	mc_sh_0059	mc_sh_0058	mc_sh_0057	mc_sh_0056	mc_sh_0055	mc_sh_0054
McMichael & Bush, 2019												
-3.09, -60.07	-3.09, -60.07	-3.09, -60.07	-3.09, -60.07	-3.09, -60.07	-3.09, -60.07	-3.09, -60.07	-3.09, -60.07	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06	-3.11, -60.06
1940, 60	1260, 40	1150, 40	1130, 40	1100, 30	1050, 40	950, 30	950, 40	2310, 120	1300, 40	1250, 80	1080, 40	1070, 50
1709 - 1939	1055 - 1192	928 - 1074	929 - 1061	921 - 990	799 - 967	744 - 908	740 - 915	2003 - 2545	1074 - 1271	962 - 1275	901 - 994	800 - 993
shcal13												

mc_sh_0080	mc_sh_0079	mc_sh_0078	mc_sh_0077	mc_sh_0076	mc_sh_0075	mc_sh_0074	mc_sh_0073	mc_sh_0072	mc_sh_0071	mc_sh_0070	mc_sh_0069	mc_sh_0068
McMichael & Bush, 2019												
-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08	-3.08, -60.08
1730, 90	1550, 40	1440, 70	1370, 40	1360, 50	1350, 30	1350, 40	1340, 40	1330, 40	1320, 60	1310, 40	1290, 30	1290, 40
1400 - 1754	1311 - 1488	1176 - 1433	1177 - 1309	1159 - 1309	1181 - 1294	1171 - 1303	1166 - 1299	1158 - 1294	1066 - 1298	1086 - 1274	1072 - 1192	1069 - 1197
shcal13												

shcal13	3237 - 3409	3170, 30	-8.863, -64.062	McMichael & Bush, 2019	mc_sh_0159
shcal13	2699 - 2998	2730, 75	-8.863, -64.062	McMichael & Bush, 2019	mc_sh_0158
shcal13	1313 - 1476	1550, 30	-8.863, -64.062	McMichael & Bush, 2019	mc_sh_0157
shcal13	1056 - 1185	1250, 30	-8.863, -64.062	McMichael & Bush, 2019	mc_sh_0156
shcal13	973 - 1271	1250, 70	-3.11, -60.06	McMichael & Bush, 2019	mc_sh_0084
shcal13	1985 - 2154	2120, 40	-3.08, -60.08	McMichael & Bush, 2019	mc_sh_0082
shcal13	1705 - 2085	1980, 80	-3.08, -60.08	McMichael & Bush, 2019	mc_sh_0081